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UNIVERSITY OF ALBERTA

INTERACTION OF BURNING AND HERBIVORY IN ASPEN COMMUNITIES IN ELK ISLAND NATIONAL PARK, ALBERTA

BY

EDWARD W. BORK

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of **MASTER OF SCIENCE**

IN

WILDLIFE AND RANGELAND RESOURCES

DEPARTMENT OF ANIMAL SCIENCE

EDMONTON, ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled THE INTERACTION OF BURNING AND HERBIVORY IN ASPEN COMMUNITIES IN ELK ISLAND NATIONAL PARK, ALBERTA submitted by EDWARD W. BORK in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in WILDLIFE AND RANGELAND RESOURCES.

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Abstract

A study was undertaken in the Elk Island National Park area of central Alberta to determine the synecological importance of the area's physical environment and management factors. Uncultivated areas outside the Park, and inside under both burned and unburned conditions, were sampled and analyzed using canonical correspondence analysis (CC), a multivariate technique. The majority of variation in species composition among sites could be explained by topographic position, the level of herbivory, and prescribed burning.

Herbivory was generally the dominant disturbance factor affecting vegetation. Inside the Park, the shrub stratum was markedly shorter and produced less browse. The tree overstory also was more intermittent in the landscape, skewed in favour of larger Populus tremuloides (aspen) trees, and generally lacking regeneration. Mature forms of some browse species, including Amelanchier alnifolia (saskatoon) and Prunus spp. (cherry), were absent inside the Park.

Whereas burning affected the vegetation across the landscape less uniformly, it increased herb production and shrub stem density. Rubus idaeus (wild red raspberry) and Lathyrus ochroleucus (yellow peavine) increased in burned areas.

Topographic position was a dominant physical site factor, interacting significantly with the level of herbivory and fire. A greater abundance of invader species was documented inside the Park, particularly on south aspects. Whereas burning had the greatest impact on vegetation at the crest position, it had little impact on north facing slopes.

From a classification of sample sites using two-way indicator species analysis (TWINSPAN), six community types were identified. These types were interpreted as being the result of interactions among herbivory, fire and forest succession. Communities included a single grassland on south facing slopes inside the Park, two mature Populus tremuloides types originating on north slopes inside and outside the Park, respectively, and three mid successional types. Of the latter, one is represented by sites outside the Park and another is found on burned areas within the Park. Each community type was

characterized by a particular combination of important environmental factors, indicator plant species, and structure to the overstory and understory vegetation.

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Table of Contents

1. Introduction 1
2. Literature Review 4
    2.1 Parkland Vegetation Classifications 4
        2.1.1 Grasslands 4
        2.1.2 Shrub and Forestlands 5
    2.2 Parkland Ecology 5
        2.2.1 Climate and Soils 6
        2.2.2 Disturbances 6
            2.2.2.1 Fire 6
            2.2.2.2 Herbivory 8
    2.3 Multivariate Analysis Techniques 9
        2.3.1 Indirect Gradient Analysis (Ordination) 9
        2.3.2 Direct Gradient Analysis 11
        2.3.3 Classification 11
3. Study Area 13
    3.1 Location and Development 13
    3.2 Fire History 13
    3.3 Climate 15
    3.4 Geomorphology and Soils 15
    3.5 Flora 16
    3.6 Fauna 17
    3.7 Ungulate Management 17
4. Methods 18
    4.1 Field Sampling 18
        4.1.1 Catena and Transect Establishment 18
        4.1.2 Environmental Sampling 20
        4.1.3 Vegetation Sampling 21
    4.2 Data Analysis 24

5. Results 30
5.1 Ordination of Plant Communities 30
5.2 Vegetative Response to Disturbance and Topographic Position 37
5.2.1 Overstory 37
5.2.2 Understory Vegetation 43
5.2.2.1 Species Diversity 43
5.2.2.2 Shrub Layer 46
5.2.3 Current Annual Production 49
5.3 Soils 55
5.4 Classification of Plant Communities 57
6. Discussion 64
6.1 Community Classification 64
6.1.1 Grasslands 69
Community A: (Populus tremuloides) / Poa pratensis / Calamagrostis canadensis 69
6.1.2 Mature Stands 71
Community B: Populus tremuloides / Corylus cornuta / low herb 72
Community C: Populus tremuloides / Corylus cornuta / mixed herb 73
6.1.3 Mid Successional Stands 73
Community D: Populus tremuloides / tall mixed shrub / tall herb 75
Community E: Populus tremuloides / low mixed shrub/ Calamagrostis canadensis 75
Community F: Populus tremuloides / low mixed shrub/ Calamagrostis canadensis - Lathyrus ochroleucus 77
6.2 Environment 78
6.2.1 Geomorphology and Soils 78
6.2.2 Disturbances 80

6.3 Forest Overstory 83
6.4 Understory Response 90
6.4.1 Species Diversity 90
6.4.2 Herb Layer 93
6.4.3 Shrub Layer 96
6.5 Forage Production 100
6.6 Summary and Management Implications 102
6.6.1 Summary 102
6.6.2 Management Implications 103
6.6.2.1 Landscape Considerations 103
6.6.2.2 Vegetation Management Considerations 107
6.6.2.3 Ungulate Management Considerations 110
6.7 Additional Research 113
7. Literature Cited 114
8. Appendices 127
Appendix I: Review of environmental and vegetative data collected 128
Appendix II: Standard error of the means for EINP data 130
Appendix III: Two-way site by species table derived from the analysis of the Elk Island data using TWINSPAN 131
Appendix IV: Conceptual soil profile descriptions for Elk Island study 121
Appendix III: Soil horizon thicknesses, soil pH, and organic matter by disturbance and position 136

List of Figures

Figure Page

Figure 1: Location of EINP in relation to the surrounding ecoregions 14
Figure 2: Location of catenas in and around EINP 19
Figure 3: Canonical correspondence analysis of sample sites and environmental variables 32
Figure 4: Correspondence analysis biplot of sample sites 33
Figure 5: Canonical correspondence analysis biplot of subset environmental variables and species whose variance explained exceeds 20% on the first two axes 35
Figure 6: Stem frequencies by diameter class under various disturbances 39
Figure 7: Stem frequencies by diameter class inside the Park 41
Figure 8: Stem frequencies by diameter class on the controls 41
Figure 9: Total tree densities under various disturbances 42
Figure 10: Canopy cover under various disturbances 42
Figure 11: Invader species diversity under various disturbances 45
Figure 12: Species richness under various disturbances 45
Figure 13: Total shrub stem densities under the various disturbances 47
Figure 14: Shrub height indices under the various disturbances 47
Figure 15: Composition of total current annual production by disturbance and position 51
Figure 16: Grass current annual production 52
Figure 17: Forb current annual production 52
Figure 18: Twig current annual production 52
Figure 19: Leaf current annual production 52
Figure 20: Total current annual above ground production 54
Figure 21: Frequency of soil types by disturbance and position 56

Figure 22: Dendrogram of TWINSPAN analysis 58
Figure 23: Correspondence analysis biplot of sample sites, community types, and environmental variables 61
Figure 24: Correspondence analysis biplot of sample sites, derived community types, species, and stand factors 63
Figure 25: Potential state and transition model for Elk Island community types 66
Figure 26: Sample layout of communities in the landscape under various disturbances 68

List of Tables

Table Page

Table 1: Sample analysis of variance used on the vegetative data 27
Table 2: Results from the forward selection of environmental variables using canonical correspondence analysis 31
Table 3: Density, basal area, and canopy cover of the tree overstory by disturbance and topographic position 38
Table 4: Species diversity, species richness, shrub density, and shrub height index by disturbance and topographic position 44
Table 5: Grass, forb, browse, and total current annual production by disturbance and topographic position 50
Table 6: Major species found in the communities of EINP 59
Table 7: Summary of environmental factors within TWINSPAN community types 62

List of Plates

Table Page

Plate 1: Community Type A 70
Plate 2: Community Type B 70
Plate 3: Community Type C 74
Plate 4: Community Type D 74
Plate 5: Community Type E 76
Plate 6: Community Type F 76

1. INTRODUCTION

The aspen parkland covers approximately 8% of the province of Alberta (Strong 1992). The region's climate and vegetation suggest that the area is a transition zone from open prairie in the south to boreal forest in the north (Moss 1932). Plant communities form a complex mosaic within the parkland landscape and include a variety of forests, shrublands, grasslands, and wetlands. This diversity among vegetation types is thought to be created by environmental variability; however, considerable controversy exists when attempting to interpret the past environment of this forest-grassland zone (Pettapiece 1969).

Since the turn of the century, most of the parkland has been heavily impacted by settlement and agricultural use. These processes led to the widespread suppression of wildfire, which resulted in a general increase in the amount of aspen cover (Moss 1932). In some areas where the native parkland remains, the forest-grassland complex once representative of the region, has been replaced by a near continuous cover of forest in the absence of disturbance (Anderson and Bailey 1980).

Elk Island National Park (EINP) is located in the heart of the parkland region in central Alberta. Although this area was classed by Strong (1992) as an outlier of the lower boreal mixedwood ecoregion, some debate has occurred concerning whether this area should be classified as aspen parkland, boreal forest, or transitional between the two (Blyth and Hudson 1987). Deciduous tree cover currently makes up the largest portion of the Park's rangelands. These forests are important because they provide wildlife with high quality habitat, offering protective and thermal cover, along with a source of forage. These forests are biologically diverse, ecologically complex, and productive with respect to forage. Despite their importance, however, little detailed information has been compiled on them, such as their inherent physical and vegetative characteristics, synecology, and response to disturbances, including those involving the actions of Park management.

The degree of resource management required in EINP is significant because of the area's small size, fenced perimeter, and abundant populations of several species of

herbivores. A semi-closed system such as this poses many questions in ungulate and vegetation co-management, particularly given the prominent impact of foraging on vegetative communities (Stoddart et al. 1975; O'Connor 1991). This is further complicated by the Park's requirement to meet the mandate and objectives of the National Parks Act. Establishing an integrated management program in an ecologically and socially acceptable manner, while still preserving the unique and natural features of the Park, has been a difficult and often controversial task. The result is that comprehensive strategies of ungulate population control and range restoration using prescribed fire have been incorporated into the Park's management.

Although fire was once viewed as a destructive and unnecessary factor in the management of national parks, recent perceptions are beginning to view fire as a positive, and even intrinsic, part of the ecosystem (Van Wagner and Methven 1980; Van Wagner 1990). To effectively utilize fire in natural resource management, however, managers need to learn how to measure, predict, and interpret the biological and ecological responses to prescribed fire and wildfire (Lotan et al. 1981). Compositional changes within the herbaceous and shrub layers of an aspen forest as a result of fire have direct impacts on the plant communities' importance for wildlife (Bartos and Mueggler 1981).

Plant communities are generally the result of specific environmental factors (Krebs 1972). In addition to variation among physical factors such as topographic position, disturbances such as herbivory and fire shape each community as well. Documenting and understanding the spatial distribution of communities within the EINP landscape, as well as their response to these disturbances, is important in order to facilitate their proper management.

Ecological research on plant communities is used to support and evaluate nature conservation at international, national, and local levels (Jongman et al. 1987). The ecological research reported here documents the vegetation from several sites in and around EINP, particularly within areas which have been influenced by prescribed burning and ungulate foraging. Analysis includes an evaluation of the relative importance and the interactions among, various disturbances and physical site factors. This study investigates how these parameters collectively determine the characteristics of several forest and

grassland areas in and around EINP. This information will assist resource managers in formulating management strategies which ultimately will achieve their specific long term objectives. Potential objectives may include maximizing the amount of available cover, forage production, biological diversity, or any combination of these. In addition, information on the area's landscape ecology can be used to evaluate whether the Park has been successful in preserving a unique and sustainable ecosystem.

Specific objectives of the study were:

1. Evaluate the effects of fire and herbivory on aspen community composition, structure, and diversity.

2. Evaluate how site factors, particularly topographic position, influence the above.

3. Create, interpret, and describe a community classification for the vegetation sampled from the EINP area.

4. Determine management implications of the edaphic, ecological, and anthropogenic factors which shape plant community expression in the EINP area.

2. LITERATURE REVIEW

The aspen parkland region of central Alberta was first described in detail by Moss (1932). The area, which he called the poplar association, was seen as a transition zone from the northern and Cordilleran forests, to the prairie in the south and east. As such, the landscape consists of a mosaic of open grasslands on the drier and warmer south facing and upland slopes, with localized forests on the cooler, more moist north facing and depressional sites (Moss 1932; Strong and Leggat 1981). Strong (1992) recognized that the northern and western areas of the parkland are represented by a larger proportion of forest cover. This region is adjacent to the more moist, boreal mixedwood ecoregion.

2.1 Parkland Vegetation Classifications

2.1.1 Grasslands

Grasslands are made up of vegetative communities which consist of a mixture of herbaceous plants that are typically free of trees, shrubs, or woody vegetation. Although native upland grasslands in the aspen parkland have been documented by Coupland (1950) as dominated by Festuca scabrella*, both Festuca scabrella and Stipa - Agropyron community types are present on well drained uplands of the northern aspen parkland (Strong 1992).

Grasslands in EINP have been classified as a single type by Bishoff (1981). Hardy and Associates (1986) identified three non-native upland grassland types including Puccinellia, Poa pratensis - Achillea millefolium, and Bromus inermis - Poa pratensis types.

---

* Species nomenclature follows Moss (1983)

2.1.2 Shrub and Forestlands

A forest is a biological community dominated by trees and other woody vegetation. Both forests and shrublands form a major component of the aspen parkland. Shrublands often represent the transition zone between Populus tremuloides (trembling aspen) forests and grasslands in the parkland landscape (Moss 1932). Numerous shrubland types have been documented (Wroe 1971; Strong and Leggat 1981; Hardy and Associates 1986; Blyth and Hudson 1987; Strong 1992).

Populus tremuloides communities are generally composed of a multilayered, complex mixture of shrubs, forbs, and graminoids with high species diversity (Debyle and Winokur 1985). Although many Populus tremuloides forest types have been described in central Alberta, few are based on the inherent composition of all species. Many of the existing classifications utilize only the dominant structural species (usually trees), with the result that forests have largely been grouped into only one or two types (eg. Moss 1932; Wroe 1971; Polster and Watson 1979; Bishoff 1981; Hardy and Associates 1986; and Strong 1992). Blyth and Hudson (1987) described three poplar forest types in EINP based on canopy closure. More recent work in the boreal mixedwood ecoregion indicates that compositional differences among the understories of Populus tremuloides stands are significant enough to describe and document them separately (Downing and Karpuk 1992; Willoughby 1993a). In the northwestern United States, several comprehensive classifications of Populus tremuloides stands have been proposed culminating with that of Mueggler (1988).

2.2 Parkland Ecology

Ecology is the study of the interactions and relationships between living systems and their environment (McIntosh 1978). Community ecology concerns itself with assemblages of plants and animals living together and the environmental and historical factors with which they interact (Gauch 1982). Landscape ecology focuses on spatial patterns of vegetation and the processes related to them. It attempts to answer questions about land-

use and land management (Jongman et al. 1987).

2.2.1 Climate and Soils

In a localized area, the effect of macroclimate on plant communities is often negligible because of its relative uniformity. The role of topographic position, slope gradient, and slope aspect, however, can be important in affecting vegetative composition. Topographic position in the parkland has been shown to affect site microclimate, including soil temperature and moisture, and therefore alters the suitability of the site for the growth and establishment of specific species (Aayad and Dix 1964; Macyk et al. 1978). This in turn results in the formation of different soil types across the landscape (Acton 1965).

Upland soils in the parkland generally consist of either grassland originated black soils (Chernozemic) or gray soils (Luvisolic) of forest origin (Moss 1932). Strong and Leggat (1981) suggest that Chernozems predominate. Soils in the parkland belt are highly variable, with sites often exhibiting characteristics of both soil types because of the transitory nature of the vegetation (Moss 1932; Pettapiece 1969).

2.2.2 Disturbances

Disturbances such as wildfire and foraging have historically affected the aspen parkland (Moss 1932; Bird 1961). Recently, however, these factors have become increasingly important because contemporary disturbances are influenced and controlled by the activities of resource managers.

2.2.2.1 Fire

Few range sites with their associated plant communities have developed without being influenced by fire (Vallentine 1980). The deliberate use of fire dates back to presettlement times when indigenous peoples inhabited the plains (Nelson and England

1971).

Fire ecology is the study of the effects of fire on the environment, and on the interrelationships of the plants and animals found living there (Komarek 1962). A recent decrease in the frequency and intensity of wildfire has interrupted the maintenance of the parkland ecosystem and allowed forest succession to accelerate (Moss 1932; Rowe and Scotter 1973). Bailey and Wroe (1974) observed a 4.8 to 8% increase in aspen cover between 1907 and 1966 in southwestern Alberta while Scheffler (1976) documented a major increase of about 0.76% per year in east central Alberta. Prescribed fire has been used to kill or suppress undesirable plant species (Wright 1974). Prescribed burning is the systematically planned burning of selected areas under the appropriate conditions, for the purpose of accomplishing a set of specific benefits (Vallentine 1980). Reasons for its use are discussed by Wright (1974) and Vallentine (1980) and include achieving changes in species composition, forage production, forage quality, or the distribution of grazing animals. The conversion of forested areas to open grasslands is a major reason for using prescribed fire in central Alberta (Anderson and Bailey 1979; Anderson and Bailey 1980; Bailey et al. 1990).

Both the frequency and severity of fire affects the vegetative composition of a community (Wright 1974). Burning promotes those species that are adapted to withstand fire or invade burned areas. Daubenmire (1968a), Anderson and Bailey (1979), and Brown and Debyle (1989) all indicate that burning favours forbs. While burning can replace forest with grassland, important native grasses can decline in composition and production (Anderson and Bailey 1980). These same investigators also found that while burning generally reduced shrub cover, the density of fire adapted shrub species actually increased. Quintilio et al. (1991) recorded a decline in Populus tremuloides and Corylus cornuta, and an increase in Calamagrostis canadensis and a variety of other forbs on a prescribed burn in north central Alberta. They also concluded that low intensity fires had little or no effect on the overstory, but under moderately intense fires tree mortality was inversely related to stem diameter.

The production response in the understory of Populus tremuloides communities exposed to fire is generally positive. Brown and Debyle (1989) found that burning

increased grass and forb production. Bartos and Mueggler (1981) found that understory production generally increased in burned communities, with grass and forb production increasing and shrub production decreasing.

As described by Rowe and Scotter (1973), the chief influence of physiography on fire is exerted through the control of surface moisture. Landforms that have dry surfaces either due to their topographic position or relief are the most susceptible to fire provided they have continuous vegetative cover.

2.2.2.2 Herbivory

Historically, native ungulates have depended on the habitat provided by the aspen parkland (Blyth and Hudson 1987). Bison in particular, were abundant throughout western Canada in the years before settlement intensified. Large herds moved southward onto the open plains during the summer months, and retreated north and west into the parkland and boreal forest in the late fall, where they converged and congregated on specific locations for winter habitation (Morgan 1980). EINP was likely one of these wintering sites. Prehistoric man's primary dependency on these vast herds committed him to maintain a close relationship with them (Morgan 1980). These yearly migrations on the plains took place until dwindling bison numbers prevented its continuance. Today, while much of the parkland is under cultivation, grazing by livestock and wildlife continues to occur on native and cultivated lands.

Ungulate use of an area is often under the direct and indirect control of resource managers. Controlled harvests are one method of manipulating stocking rates and utilization levels. Foraging intensity is also dependent on physical factors such as topography, with heavier grazing often associated with depressional areas and flatter slopes (Mueggler 1965).

The response of individual plants to foraging is dependent on their morphological and physiological adaptations, with community composition largely determined by grazing pressures from major herbivores (Stoddart et al. 1975). Populus tremuloides communities which have been heavily grazed change gradually to a mix of fewer species, and a greater

abundance of plants of low palatability (Mueggler 1985). Weatherill and Keith (1969) found the overstory was affected little in central Alberta by ten years of cattle grazing, but that taller herbaceous plants in the understory were replaced by shorter, often exotic species. Willoughby (1993a) found that Poa pratensis, Phleum pratense, and Trifolium repens dominated the understory of heavily grazed Populus tremuloides communities on Alberta's eastern slopes.

Populus tremuloides forests provide forage for livestock and native ungulates throughout most of western North America. Production is highly variable and dependent on many factors. In the United States, production in the understory of many stands has been documented to be as high as 2300 kg/ha (Mueggler 1985). In western and northern Alberta, understory production has been found to range from 448 to 2022 kg/ha (Willoughby 1993a).

2.3 Multivariate Analysis Techniques

Data used in community and landscape ecology are multivariate in nature because each sample site is described by the abundance of several species which are affected by numerous environmental factors (Gauch 1982). Multivariate analysis treats data as a whole by summarizing it to reveal the underlying structure (Gauch 1982). Multivariate methods can be divided into three groups: direct gradient (or regression) analysis, indirect gradient analysis (or ordination), and classification (or cluster analysis) (Jongman et al. 1987).

Direct gradient analysis deliberately arranges samples in terms of one or more known environmental factors (Whittaker 1973). By contrast, indirect gradient analysis and classification techniques start with the analysis of community data alone and use environmental data for subsequent interpretation (Gauch 1982).

2.3.1 Indirect Gradient Analysis (Ordination)

Ordination arranges sample sites along an axis on the basis of species composition (Jongman et al. 1987). The objective is to arrange sites that have similar species composition close together, while positioning sites with differing species composition far apart. This allows differences among sites to become more apparent and facilitates interpretation of the major axes.

Correspondence analysis (CA), detrended correspondence analysis (DCA), and principle components analysis (PCA) are indirect gradient analysis techniques popular among community ecologists (Jongman et al. 1987). Indirect techniques execute the ordination without the use of explanatory variables and thus require less data to undertake. Methods of correspondence analysis (CA and DCA) assume a unimodal response model for individual species abundances among sites, while PCA implies a linear response model (Jongman et al. 1987). Ecological data collected over a large range of habitat variation usually require non-linear models (Jongman et al. 1987). The model that is more appropriate can be determined by the length of the ordination axis. Lengths over four units generally require unimodal techniques (Jongman et al. 1987).

Detrended correspondence analysis was developed to overcome two potential problems with standard correspondence analysis; compression of the ends of the axis relative to the middle, and the arch effect, which is the systematic relation of the second axis to the first (Hill and Gauch 1980). Detrending involves rescaling the axis scores by dividing the first axis into segments and adjusting the second axis scores so that they have an average of zero (Gauch 1982). Recently Minchin (1987) found that DCA can flatten out some of the variation within gradients presumably due to the instability created by detrending. While Jongman et al. (1987) advise against routine use of detrending, others suggest that detrending is not needed in direct gradient analysis if the set of environmental variables is first reduced to the essential ones (Ter Braak and Prentice 1988). A comparison between the two may be the most appropriate method of evaluating the effectiveness of using DCA versus CA.

2.3.2 Direct Gradient Analysis (Constrained Ordination)

Canonical correspondence analysis (CC) is a multivariate direct gradient analysis technique which combines aspects of ordination and regression. The aim of this technique is to detect the main patterns in the species data that can best be explained by the optimum linear combination of the observed environmental variables (Jongman et al. 1987). The ordination of species and sites is therefore constrained by the environmental data.

A potential drawback of direct gradient analysis is that environmental conditions are difficult to characterize exhaustively (Jongman et al. 1987). Comparisons of indirect and direct gradient techniques can be used to determine if any important environmental variables have been overlooked (Jongman et al. 1987).

2.3.3 Classification

Classification is the assignment of entities to classes or groups (Gauch 1982). Land must be classified to provide an effective basis for management and land use planning (Cook and Stubbendieck 1986). Vegetation classification can be summarized as the systematic documentation of plant communities into organized groupings for scientific or practical purposes.

An ecological classification of rangelands deals with physical and environmental factors including precipitation, topography, soils, and broadly defined vegetative components (Stoddart et al. 1975). A plant community consists of a specific combination of plant species found inhabiting an area, which depend on their environment and influence one another, as well as modify their own environment (Mueller-Dombois and Ellenberg 1974). Plant communities are classified through the interaction between a phytosociologist and the vegetation (Whittaker 1962). Community taxonomy therefore depends not only on the composition, physiognomy and environment of plant communities, but also on the expertise and objectives of the ecologist.

Specific objectives of vegetation classification are to provide internal information on

the occurrence of species between sites and to establish community types for descriptive studies (Whittaker 1973; Gauch 1982; Jongman et al. 1987). Mueller-Dombois and Ellenberg (1974) point out that it is important to differentiate between an actual plant community in the field and the abstract community type with which it may be associated. Plant communities are summarized by way of community types which are derived from classification techniques.

Two general methods of cluster analysis can be used to classify sites and species (Jongman et al. 1987). Agglomerative techniques progressively group sites together to form fewer, more general associations. Divisive methods start with one group containing all sites and divide it into two subgroups. Each of these is then divided further, eventually producing numerous, highly specific groupings.

Methods of classification can be further subdivided based on whether they are hierarchial or not (Jongman et al. 1987). Hierarchial methods lead to an arrangement of samples in a tree diagram, or dendrogram, reflecting both the successive steps and the presumptive relationships among classes (Whittaker 1978). To distinguish a final set of classes on the basis of a dendrogram requires the establishment of a stopping rule (Whittaker 1978). Non-hierarchial methods do not impose such a structure on the data and handle redundancy, noise, and outliers in the data (Jongman et al. 1987).

One of the most commonly used programs in ecology for the classification of community types is Two Way Indicator Species Analysis (TWINSPAN) (Jongman et al. 1987). This program uses a polythetic, divisive, hierarchial classification procedure (Hill 1979). TWINSPAN arranges multivariate data in an ordered two-way site by species table using an internal iteration algorithm, and utilizes differential or indicator species to split the collection of sample sites into two groups. Processing of the data is done through a process of coding where species abundances are converted into classes called pseudospecies (Hill et al. 1975). Since no formal stopping rule exists, creation of the final communities remains up to the ecologist through interpretation of the dendrogram. Among the numerous advantages of TWINSPAN are its integrated classification of both samples and species, and the relative ease with which the resulting dendrogram can be interpreted (Gauch 1982).

3. STUDY AREA

3.1 Location and Development

Elk Island National Park is a 196 km^2 area situated in the Beaver Hills of central Alberta, approximately 37 km northeast of Edmonton, Alberta. The Park is divided into two areas by a major highway; the main Park of 136 km^2 to the north, and a 59 km^2 isolation area to the south (Blyth and Hudson 1987). EINP is part of an island of relatively undeveloped landscape, surrounded by intensively cultivated agricultural lands. The Park is situated in the north central portion of the parkland, south of the main boreal mixedwood forest (Figure 1).

The original Park was first established in 1906, when an area was fenced to act as a game preserve to protect one of the last remaining wapiti herds in central Alberta. The subsequent introduction of plains bison took place in 1907. In 1913, the area officially became Elk Island Dominion Park and in 1930 became a National Park.

Major expansions of the original area occurred in 1922 and 1947 when the area south of Astotin Lake to highway 16, and the Isolation Area, respectively, were added (Blyth and Hudson 1987). Minor additions also took place in 1956 and 1978.

3.2 Fire History

Before extensive settlement, the Beaver Hills were routinely subject to wildfire. These were caused by both natural phenomena such as lightning, and by indigenous peoples. Indians used fire to produce lush regrowth for their horses to graze, and to attract bison into the area (Bird 1961; Thomas 1977). Since a comprehensive and detailed fire history is unavailable for the EINP area during presettlement times, the actual role of fire in the region at that time remains speculative. More recent records indicate that most of the Park was heavily forested until a very large, severe fire in 1895 removed most of the forest cover in the area (Kjorlien 1977). That fire, with the exception of several small, low intensity grass fires and one larger fire north of Astotin Lake in 1946

Figure 1: Location of EINP in relation to the surrounding ecoregions (After Strong 1992).

(Blyth and Hudson 1987), marked the end of widespread burning in the main Park. Intensive agriculture surrounding the Park and advanced fire suppression practices have combined to limit the occurrence of wildfire.

Fire continued to be of minor importance until 1979 when a prescribed burning program was initiated (Deering 1987). Since 1979, about 16 major fires have been carried out, with at least six occurring in the study area. Park records indicate that these fires occurred in 1982, 1983, 1988, 1989, and 1991. The latest fire took place in the spring of 1993, less than one year after the data were collected for this study.

3.3 Climate

The climate of the EINP area is classed as cool continental, with cold winters and warm summers (Bowser et al. 1962). Mean temperatures average -16.5°C and +16.4°C for January and July, respectively (Blyth and Hudson 1987), with absolute temperatures ranging from -45 to +38°C. Annual precipitation varies from 400 to 450 mm, with about three quarters falling as rain during the summer growing period (May to August), and one quarter falling as snow from October to mid May. Total annual snowfall is variable ranging from 52 to 222 cm in the period from 1982 to 1991 (Parks Canada 1992).

3.4 Geomorphology and Soils

EINP and the Beaver Hills are part of the Cooking Lake moraine which was deposited after the retreat of the Wisconsin ice sheet some 10,000 years ago. This landform rises approximately 30-50 meters above the surrounding plains. The predominant geologic material found throughout the moraine is glacial till with isolated deposits of aeolian and lacustrine origin.

Topographically, the area is characterized by gently to strongly undulating hummocks. Depressional sites are often flooded and form moist fens, sloughs, marshes, or shallow lakes. Soils in the area reflect the variable parent materials, topography, and vegetative cover. Upland soils in the Park are classified as belonging to either the Dark Gray

Luvisol subgroup or the more predominant, Orthic Gray Luvisol subgroup (Crown 1977). These soils are found under semi-open shrublands and forests, respectively. Depressional sites with impeded drainage are characterized by Humic Luvic Gleysols, Rego Gleysols, and Organics (Crown 1977).

3.5 Flora

The upland vegetation in the study area is dominated by Populus tremuloides (trembling aspen) forest. Populus balsamifera (balsam poplar) is codominant on some sites, particularly those which are more moist. Betula papyrifera (white birch) is also present in some areas, but rarely forms a major component of the overstory. Although sporadic areas of the Park have Picea glauca (white spruce), either as a codominant or subdominant, this tree species was rare within the study sites. Picea mariana (black spruce) is limited to the numerous depressional fens scattered throughout the Park.

The understory of the deciduous forests is highly diverse and often stratified. Tall shrubs such as Amelanchier alnifolia (saskatoon), Prunus pensylvanica (pincherry), Prunus virginiana (chokecherry), Salix spp. (willow), and Alnus crispa (alder) are present, but vary significantly between sites. A low shrub layer is prominent throughout most of the Park and includes Corylus cornuta (beaked hazel), Rosa acicularis and Rosa woodsii (prickly and wild red rose), Rubus idaeus (wild red raspberry), Viburnum edule (low bush cranberry), Cornus stolonifera (red-osier dogwood), Symphoricarpos occidentalis (western snowberry), Ribes spp. (gooseberry), and Lonicera spp. (honeysuckle).

Tall and low forb components make up a large portion of the total vegetative cover. Tall forbs such as Solidago spp. (goldenrod), Epilobium angustifolium (fireweed), and Aralia nudicaulis (sarsaparilla) are abundant on many sites while a rich mix of low forb species make up the lowest strata of the understory. Major grasses include Poa pratensis (Kentucky bluegrass), Calamagrostis canadensis (marsh reed grass), and Carex spp. (sedges).

3.6 Fauna

The study area contains a wide variety of animal life. Numerous species of birds, rodents, and small mammals inhabit the area, either on a seasonal or year long basis. The Park supports significant populations of ungulates including Bison bison (bison), Cervus elaphus (wapiti), Alces alces (moose), and Odocoilius virginianus and Odocoilius hemionus (whitetail and mule deer) (Blyth and Hudson 1987). No major predators of any abundance are present in the Park. Although large numbers of Canis latrans (coyote) are present, they prey on smaller animals and are generally limited to scavenging on the larger ungulates.

3.7 Ungulate Management

The sizable populations of native ungulates have had a major impact on the area's vegetation since the Park's establishment. As ungulate populations increased after 1906, so did the demand for forage. This was temporarily counteracted in 1922 when the size of the main park was more than tripled. In a review of historical park journals, Blyth and Hudson (1987) cited numerous examples of how rapid forest invasion initially took place in the early years following 1922 when stocking levels were low, but as ungulate populations rapidly grew, extensive browsing and destruction of young trees began to occur. The result was that in 1928, 1934, and quite regularly thereafter until 1980, extensive animal harvests were undertaken, beginning with the bison and eventually involving wapiti and moose (Blyth and Hudson 1987). A massive 1959 harvest was large enough to reduce ungulate densities to their mid 1920's level. High ungulate populations were prevalent in the 30's, 40's, and 50's in part, because of the production of domestic hay crops used to supplement the bison herd through each winter. Later on, live trapping was also used to remove ungulates, and currently remains as the only widely used method of animal harvest. Both plains bison and wapiti are regularly trapped and removed using this technique. Present stocking rates are comparable to those witnessed in the 1940's to 1960's.

4. METHODS

4.1 Field Sampling

4.1.1 Catena and Transect Establishment

A catena is a series of consecutive ecosites within the landscape, which differ from one another by characteristics such as their inherent soils, plants and herbivores (Archer and Smeins 1991). Data were collected from four transects on each of nine catenas in and around EINP during the summer of 1992. Figure 2 presents the general location of the catenas.

Each catena consisted of a landscape sequence which followed the hummocky topography that is typical of the Park. Four linear transects were established on each catena, one across the slope at each of four topographic positions to promote uniformity between the subsampling quadrats. Positions included the lower south (or toe) slope, south facing slope, crest position, and north facing slope. Transects were fifty meters in length, and were permanently marked with steel pegs at either end. The starting point of each transect was randomly located. A tape measure was then rolled out 50 meters perpendicular to the slope. After tightening, the second pin was anchored. A general azimuth reading was taken on the final position of each transect, originating from the east side.

Selection of the catenas was done on the basis of their historical exposure to disturbance, irrespective of the current vegetation. The only restrictions were that sample sites had to be available on slopes with each of the four desired aspects, and they needed to be large enough for effective transect establishment. The selected catenas were therefore those with relatively prominent south and north facing slopes. This maximized the area available for sampling and the affect of topographic position within each catena.

Three catenas were situated outside the Park to represent controls. This area can be regarded as a control because of the lack of major disturbances, specifically prescribed fire and intense herbivory. Although some use by native ungulates does occur, past

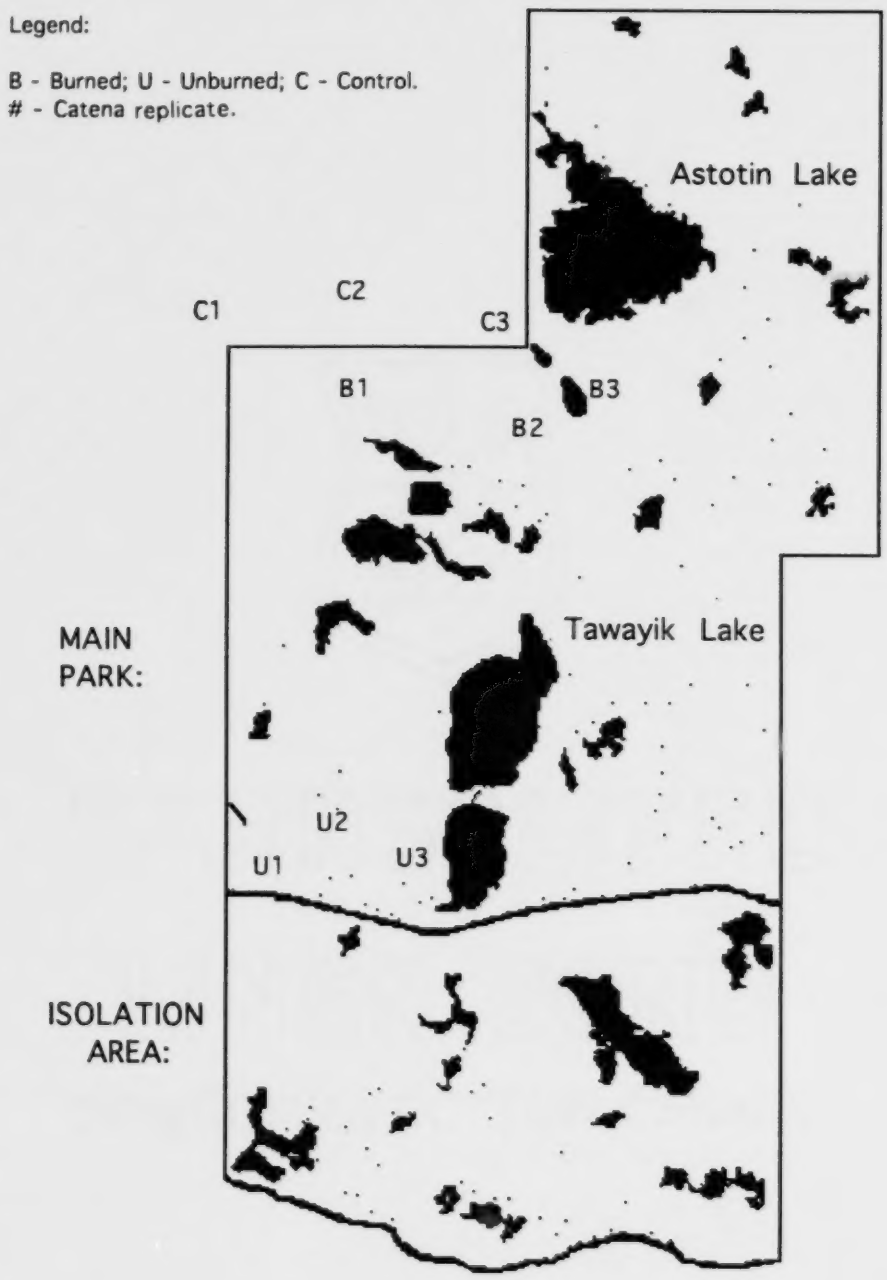


Figure 2: Location of catenas in and around EINP.

foraging pressures have been low. Controls have also been free of livestock grazing for a minimum period of 20 years (Helen Simmons, local landowner, personal comm. 1992), and have not been subject to recent wildfire.

Six catenas were located inside the Park to represent high levels of ungulate foraging. This intensity is the result of sustained high stocking levels since the Park was expanded to include the study area in 1922. Three catenas were in areas which had been subjected to a series of prescribed burns over the period 1982 to 1991. Each catena selected was burned at least twice according to park records. The remaining three catenas were situated on unburned areas within the Park.

4.1.2 Environmental Sampling

Environmental data included any information that was used to explain the variation in species composition among plant communities. In addition to recognizing the type of disturbance occurring at each transect, other environmental data were collected on the physical site factors such as the general topographic position, percent slope (averaged for transect) and various soils data. A complete review of all the environmental and vegetative data collected and analyzed is in Appendix I.

A soil pit was dug at the center of each transect on the downslope side (south side for toe, south, and crest positions) to identify the soil Order and Great Group. Soil nomenclature followed that of Agriculture Canada (1987). Dry soil profiles were described with respect to the soil horizon thicknesses (cm), and colors of the surface (A and B) horizons. Other general observations were made including the presence of stones, roots, mottles, gleying, or macrostructure. In addition, each profile was checked, particularly the litter-fibric-humic (LFH) horizon, for the presence of charcoal deposits as evidence of past exposure to fire. Photographs were taken of each pit in the moist and dry state.

Soil samples were taken in late summer when the horizons were dry and easier to identify. Samples were collected from a depth of approximately 5 cm, which generally placed the sample in the Ahe horizon. In those soils where the bottom of the Ahe was

less than 5 cm from the surface, the bottom of the Ahe was sampled for consistency.

The soil samples were air dried and analyzed at the Alberta Agriculture Plant and Soil Laboratory. Lab analyses included the determination of percent organic matter, pH, and texture. Texture of the samples was done using the hydrometer method which produced quantitative data on the percentage of sand, silt, and clay.

4.1.3 Vegetation Sampling

Sampling of the vegetation was done in two phases, the overstory and understory. Tree overstory data were collected from a belted macroplot 50 by 4 meters in dimension (200 m^2) using the transect as the long axis. Two meters on either side of the transect formed the macroplot. Trees with a minimum height of 3 meters, and whose center was within the plot, were counted and measured.

A diameter tape was used at the author's waist height to determine the diameter of each tree in cm. Basal area of each tree was then calculated:

$$\text{Basal Area } (m^2) = (\text{Tree Diameter in cm} / 2)^2 \times 3.1416$$

A total basal area per transect was determined by summing the basal areas for all trees and converting this to m^2/ha:

$$\text{Basal Area } (m^2/ha) = (\Sigma (\text{Basal Area / Tree})) \times 50$$

In each burned macroplot, burn scorch heights were measured for each tree to the nearest centimeter using a ruler. These heights were then averaged for all trees in the macroplot to obtain an estimate of the average minimum burn intensity per transect, which was used in the community evaluation. Scorch heights are an important component when determining fire intensity (Alexander 1982), and have been shown to be strongly correlated to the direct impact of fire on tree damage and mortality (Van Wagner 1973). Scorch heights could not be measured for two transects in the burned area because these south slopes were devoid of trees on the south aspect. Therefore, the average height from the south slope on the second catena was used for all three burned south slopes in the ordination analysis. This was done primarily so that burning could be entered as a quantitative variable rather than as a nominal one. Qualitative descriptions of fire

intensity have several shortcomings, including varying among seasons, individuals, and years (Alexander 1982). The impact of topographic position on fire intensity through the control of surface moisture and the distribution and ignition of fuel, indicates that fires occurring at the same position within a landscape often will have similar intensities.

Live overstory canopy cover was estimated using ocular techniques in conjunction with the line intercept method (Cook and Stubbendieck 1986). In this method, all segments of the linear transect which intercepted with the polygonal canopy of the live overhead trees, were recorded to the nearest 0.1 m. The total intercept length was then summed for the transect and converted to a percentage:

$$\text{Canopy Cover (\%)} = ((\sum \text{ Segment 1 (m) + Segment 2 (m) + ...})/ 50) \times 100$$

The main understory vegetation sampling was conducted from July 2 to July 30, 1992, after maximum vegetative growth was attained. Each transect consisted of 15 nested subsampling quadrats at stratified intervals, beginning at the 1 meter position. Selecting the quadrat locations in advance ensured they were distributed free of surveyor bias. The starting locations of the plots were as follows; 1, 4, 8, 11, 14, 17, 21, 25, 29, 32, 35, 38, 41, 45, and 48 meters from the east end of the transect.

At each quadrat, a variety of information was collected from two nested plot frames using a variation of the technique of Daubenmire (1959). Microplots 1/5th square meter in size (50 cm x 40 cm) were used to estimate the percent polygonal canopy cover of all grass and forb species, as well as the cover of litter, moss, and bare soil. Generally, estimates below 10% were made to the nearest percent, while above this amount they were done in intervals of either 2% (those from 10% to 20%) or 5% (those over 20%). The narrow portion of the frame was placed adjacent to the transect. Direct canopy cover estimates were used instead of cover classes to avoid ambiguity in cover values which may border between classes. All species nomenclature followed that of Moss (1983). The number of different species found per transect was evaluated as species richness, along with species diversity using the Shannon method. The formula used to calculate Shannon diversity was (Shaw 1985):

$H = - \sum_i^n p_i (\log (p_i))$, where n = the total number of species, and

p_i = (abundance of species i) / ($\sum$ abundances of all species).

In addition to overall diversity, the portion of total diversity which was attributable to invader species was determined. For simplicity, and because a primary objective of the Park is to protect native biodiversity, those species which have been introduced to North America were considered invaders. Photographs were taken along each transect to aid in documenting each plant community.

The microplots were also used to determine the density of live stems of each shrub species. All stems whose root crowns originated within the microplot were counted. Individual stems were recognized as those which were growing independently at the surface of the LFH layer. Because the total sampling area per transect was 3 square meters (15 x 0.2 m^2), the total stem count was then divided by 3 to obtain a density per m^2. The maximum shrub height found in every microplot was also recorded to the nearest 5 cm using a ruler. Intervals were used because of the limited accuracy at which these heights could be taken. These heights were then averaged across the 15 quadrats per transect to obtain a shrub height index (cm). The percent polygonal canopy cover of all shrubs was estimated from mesoplots 1 m^2 in size overlaying each microplot.

Two production clips were taken along each transect. These clips were 50 by 100 cm (0.5 m^2) in size and located at the 6 and 43 meter locations. Clips were generally ungrazed and therefore represented maximum production. All current annual above ground production was removed and sorted into grass, forb, shrub leaf, and shrub twig components. These were oven dried for a minimum of 72 hours at 38°C and weighed. Yield conversion to kg/ha was then done:

Yield (kg/ha) = ((Clip 1(g) + Clip 2 (g))/2) x 20

4.2 Data Analysis

Ordination and cluster analysis are often used in the exploratory phase of an ecological investigation (Jongman et al. 1987). More specific techniques such as regression analysis or an analysis of variance (ANOVA) are then used to investigate specific factors in more detail.

The primary objective of this study was to evaluate the influence of environmental factors on plant communities in the aspen parkland of EINP. Direct gradient analysis is the multivariate technique which allows this investigation to be done at the community level. Therefore, ordination techniques were initially used to evaluate the impact of the environmental factors on the composition of communities.

Analysis was done using the software program canonical correspondence analysis (CANOCO) (ter Braak 1992). This program utilizes a two-way weighted averaging iterative algorithm to construct biplot (graph) axes. The general objective of the algorithm is to maximize the species variation accounted for among sample sites by maximizing the dispersion of sites along each axis. This arrangement is achieved when site and species scores eventually stabilize at a point of maximum dispersion within a two-way species by site table (Hill 1973).

All options within the CANOCO program were generally set to the defaults when running the ordination program. All environmental variables were used, except those that displayed a high degree of correlation with other environmental factors, in which case the most influential variable was used. Weighted correlations between variables indicated that percent slope was the only variable in the data set which displayed high correlations with other variables. Absolute correlations between the slope and the crest and north facing topographic positions were 0.60 and 0.56, respectively. This indicated that if the positions and slope gradient were both maintained in the analysis, the explanatory power of each would have been reduced. Slope was therefore removed as an environmental variable.

Initial analysis of the data with a unimodal method (CC) revealed that this technique would be more appropriate than a linear approach because the first axis was well over 4

standard units in length. This large dispersion indicates that the extent of habitat variation among sample sites is considerable, probably because of the variety of environmental factors investigated. To ensure that detrending was not necessary, the same data were run using Detrended CC with little impact other than a slight net loss of separation between sites. This loss, however, was attributed to the averaging within segments procedure which DCCA utilizes. It was thus concluded that the arch effect was not prevalent and that detrending was not required.

The data used to represent communities consisted of the canopy coverage of each species on all 36 transects, as well as the cover of moss and bare ground. Explanatory factors, or those environmental criteria which were used to account for the variation in species composition among sample sites, were the disturbances and various physical site characteristics. Most of the data utilized were represented by quantitative values. Nominal variables included the intensity of herbivory, topographic position, and diagnostic soil type with two, four, and three classes, respectively.

To make the ordination more understandable, a subsequent run isolated the most important explanatory variables. The forward regression option of the CANOCO program was used to select a subset of the most important environmental factors.

Parameters which aided in the interpretation of ordination included the eigenvalues, canonical coefficients, species-environment correlations, and inter-set correlations (Jongman et al. 1987). Eigenvalues were derived directly from the stabilized scores on the ordination axis and provide a relative measure of importance of each axis based on species variation explained. Even ordinations which explain only a low percentage of species variance may be very informative (Gauch 1982). Species-environment correlations indirectly measure the strength of the relationship on a particular axis between the species data and the environmental variables (ter Braak 1992). Inter-set correlation coefficients measure the relationship between an individual environmental variable, independent of the influence of others, and the species axis (ter Braak 1992). The program CANOCO also contains a Monte Carlo permutation procedure to investigate the statistical significance of environmental effects (ter Braak 1992). This procedure randomly generates a number of environmental data sets with properties similar to the one

actually being evaluated, and tests for the amount of residual variation in species data accounted for within each model. A significance test is done through an F-type statistic.

To verify that no important, independent, explanatory variables were omitted in the overall data collection process, an indirect analysis was conducted on the same data using correspondence analysis (CA). An indirect analysis is unconstrained by explanatory variables, with each axis created to maximize the amount of variation explained between sites, regardless of all environmental variables.

Interpretation of ordination results was aided through the construction of a joint biplot of the species, site, and/or environmental scores. The distance that an environmental variable is from the origin is directly related to its explanatory power, particularly with respect to the nearest axis (Jongman et al. 1987). In addition, those environmental factors which are situated close together are more likely to interact while affecting community composition.

Projection of species points onto the axis of an environmental variable which runs from the origin to the environmental coordinate determines the strength of the relation between the species and the factor (Jongman et al. 1987). To investigate the influence of the dominant environmental factors on the species themselves, all species with a minimum of 20% of their total variance explained by the first two axis' were plotted in a biplot together with the subset of environmental variables. Twenty seven species met this criteria. A complete review of the construction and interpretation of biplots is provided by Jongman et al. (1987).

Subsequent analysis using a split-plot analysis of variance (ANOVA) (Steel and Torrie 1980) evaluated the specific effects of each disturbance and position on physiognomic characters such as tree and shrub density, tree canopy cover, species richness and diversity, and current annual above ground production. Table 1 depicts the generalized analysis of variance used to investigate these differences. All stem count data were checked for normality using scatterplots before being used in the ANOVAs. Mean comparisons within the disturbances, positions, and their interactions, were done based on the least significant difference (LSD) method. All significant differences are at P=0.05 unless specified otherwise. Standard error of the means are provided for all stand

Table 1: Sample analysis of variance used on the vegetative data.

Source:	Degrees of Freedom:	Applicable F-Test:
1. Disturbance	3-1 = 2	1 vs Error A
2. Catena(Disturbance)	(3)(3-1) = 6	Error A
3. Position	4-1= 3	3 vs Error B
4. Position x Disturbance	(3-1)(4-1)= 6	4 vs Error B
5. Pos x Catena(Dist)	(4-1)(6) = 18	Error B
Total	N-1=35	

characteristics in Appendix II.

Forest stem size distributions were investigated by plotting the frequency of stems occurring in a series of incremental diameter classes within each disturbance and topographic position. An ANOVA using the interaction of diameter class and disturbance as the error term was used to evaluate the effect of the disturbances on these distributions.

The classification of plant communities was done using TWINSPAN. Similar to CANOCO, TWINSPAN also uses the two-way iterative weighted averaging algorithm. Instead of constructing biplot axes, however, it uses the diagnol arrangement of data within the two-way table to split sample sites into groupings. The final two-way table containing the groupings of TWINSPAN are provided in Appendix III.

In general, the default settings within TWINSPAN were used because although other settings were tried,the most decisive classification appeared to take place using this technique. Important default parameters included the five pseudospecies abundance cover classes from 0-2%, 2-5%, 5-10%, 10-20%, and greater than 20%. Several small alterations were done, however, to improve the classification of sample sites. The close proximity of adjacent catenas and transects to one another in the landscape resulted in high species overlap between sites. Therefore, downweighting of the lowest pseudospecies class (<2%) was utilized. Downweighting does not eliminate these species from the analysis, but gives them less emphasis thereby ensuring that the abundant random variation or 'noise' in the species data does not distort the ordination. Downweighting also decreases the sensitivity of the cluster technique to rare species which may be encountered merely by chance (Jongman et al. 1987). Pseudospecies falling in this class received half the weight of the middle classes. In addition, those pseudospecies in class five (over 20% cover) were regarded as dominants and were weighted one and a half times that of the middle classes to ensure that they received priority consideration in the analysis. Even under this setting, however, only one pseudospecies over 20% appeared as an indicator.

To aid in the interpretation of the final classification, an indirect ordination was used to examine sample sites for groupings. Indicator species, stand characters, and environmental factors were passively ordinated to help determine correlations or visible

relationships between the communities, species, and their environments. Naming of the communities is similar to the format used by Mueggler (1988) with individual species and structure of the understory (eg. tall herbs, low shrubs, tall shrubs) both taken into consideration. Final derived community types were summarized based on the vegetative information available.

5. RESULTS

5.1 Ordination of Plant Communities

The most influential environmental variables affecting the plant communities sampled included the four topographic positions, level of herbivory, influence of fire, and thickness of the Ahe horizon. The forward regression procedure within the canonical correspondence analysis (CC) indicated that each of these factors explained a significant portion of the residual species variation when selected into the subset of variables, at P=0.05. Table 2 provides the order of entry into the model and significance level of each variable.

Figure 3 depicts the resulting biplot of a CC using only the subset of variables outlined above. Eigenvalues for the biplot axes are 0.283 and 0.118 respectively, while those of the third and fourth axes are 0.077 and 0.052 (ungraphed). Therefore, although axis 1 explains the most species variation among sample sites, axes 1 and 2 combined explained a considerably larger portion of the total species variance. A significance test of the first eigenvalue using the Monte Carlo procedure within the CANOCO program indicated that the first axis explained a significant portion of species variation at P=0.01.

The amount of actual species variation explained by the first two axes alone (ie. independent of environment) were 19.9% and 8.3%, respectively. This amount decreased to 5.4% and 3.7% for the third and fourth axes. For the subset of eight environmental variables, the species - environment correlations were 89% and 80.6% on axes 1 and 2, respectively. These values were very close to the same correlations found when all environmental variables were used (92.1% and 85.6%), indicating that little of the explanatory power of the environmental variables was lost by isolating the subset of variables. Figure 4 presents the biplot of an indirect correspondence analysis (CA). Comparison to the CC biplot revealed few differences. It was therefore concluded that no critical, independent environmental variables were left out of the data collection and analysis process.

Table 2: Results from the forward selection of environmental variables using canonical correspondence analysis (CCA).

Order of Entry:	Environmental Factor:	Variation Explained:	Significance of Monte Carlo Test:	Inter-set Correlations: Axis 1:	Axis 2:
1	South Slope	17 %	P = 0.01	-.59	-.34
2	High Herbivory	13 %	P = 0.01	-.49	-.08
	Low Herbivory	* N/A	Default Entry	.49	.08
3	North Slope	12 %	P = 0.01	.58	-.42
4	Burn Scorch Height	6 %	P = 0.02	-.31	.36
5	Toe Slope	5 %	P = 0.03	-.11	.45
	Crest Slope	* N/A	Default Entry	.12	.29
6	Thickness of Ahe	5 %	P = 0.03	-.09	.36
	Thickness of Ah	Failed Entry at P = 0.17 ending Forward Selection.			

* Note: Inclusion of the second last nominal variable into the model by default results in the last nominal variable being selected as well.

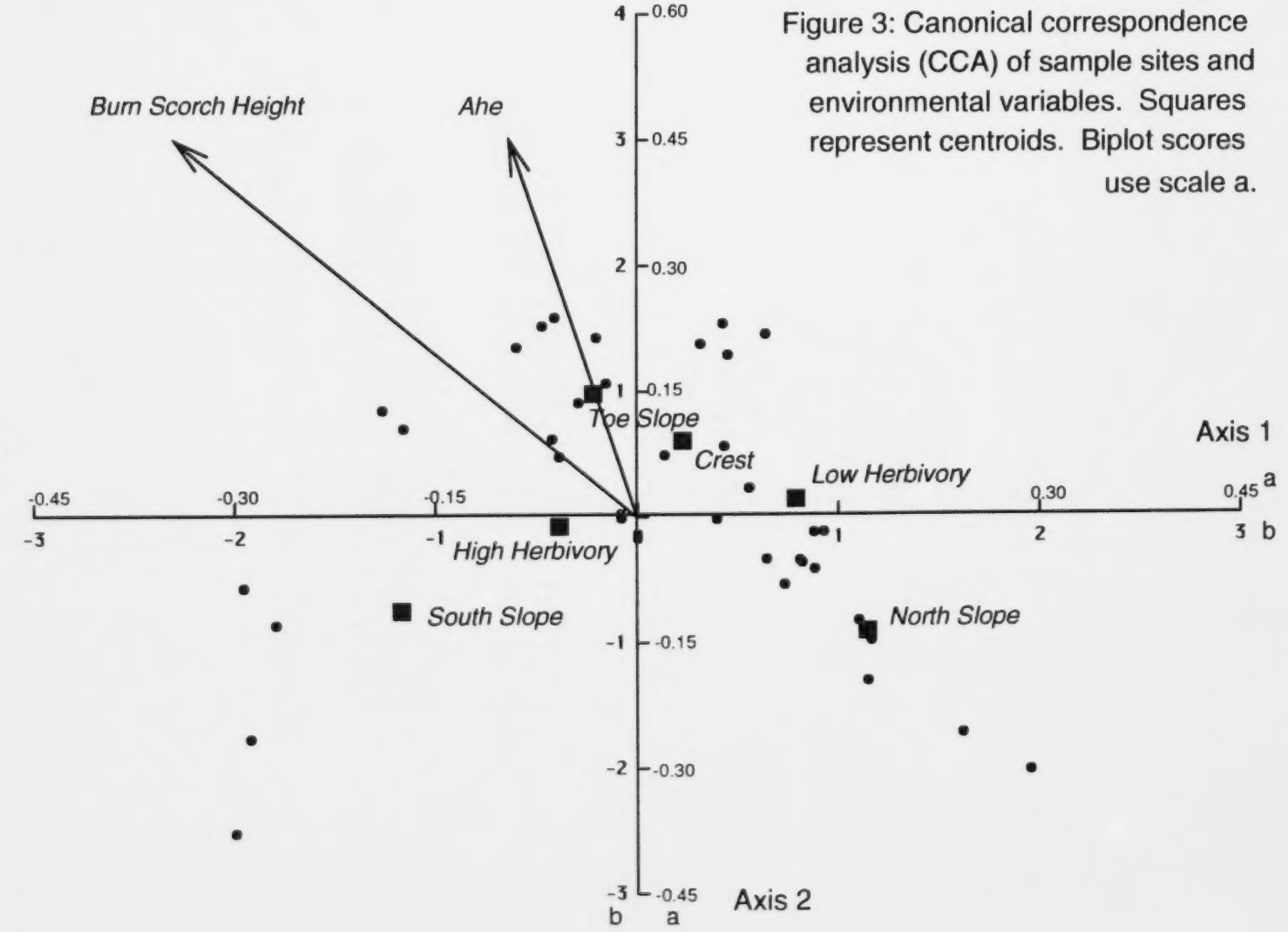


Figure 3: Canonical correspondence analysis (CCA) of sample sites and environmental variables. Squares represent centroids. Biplot scores use scale a.

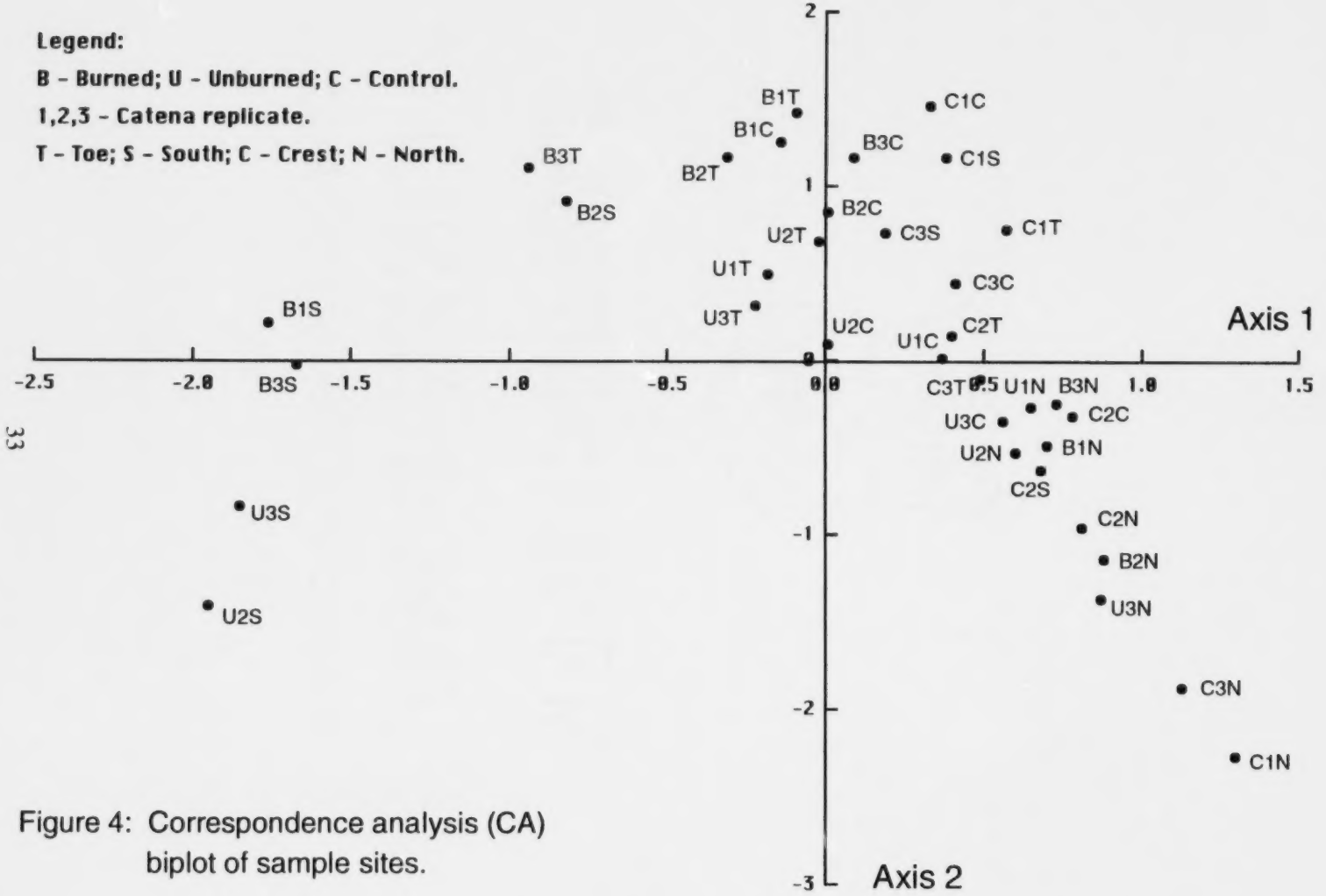


Figure 4: Correspondence analysis (CA) biplot of sample sites.

The regression revealed that the disturbances and topographic positions explained the most significant amount of species variation between sample sites. The inter-set correlations indicate that the order of importance among environmental variables in decreasing order was the south facing slope, north facing slope, level of herbivory, and burn scorch height, all of which were strongly correlated with the first axis (Table 2). Between the two disturbances, herbivory appeared to be a more important factor, entering second and accounting for 13% of the residual variation while burn scorch height entered fourth and explained only 6%. The toe slope, crest position, and thickness of the Ahe were less important on axis 1, but explained proportionately more of the variation on axis 2. This was also evident by the larger horizontal distance of the first four factors from the origin and the increased distance of the latter three variables in a vertical direction compared to their horizontal extension (Figure 3).

Interactions also appeared to occur between the topographic positions and disturbances. Evidence of this was provided by the interchanging of these factors as they were selected in the regression (Table 2), as well as by their pattern of distribution in the biplot (Figure 3). Although the disturbances and positions were quite well dispersed in the biplot, the pattern was not in simple horizontal and vertical directions from the origin. Instead, each axis was influenced by combinations of factors. Sample sites in the lower left quadrant of the biplot were closely related to the south slope and high herbivory variables. Sites on the lower right side were located closer to the low herbivory and north slope variables suggesting their association. The remaining sites were collectively scattered around the remaining environmental variables in the center of the biplot and above the origin. Of special note was the close proximity of the thickness of the Ahe horizon and the toe slope position, particularly because they lie on the same plane away from the origin.

Figure 5 contains the biplot of a CA analysis with species plotted whose variance explained by the first two axes were a minimum of 20%. Species identification codes were derived by combining the first four letters of the genus name, and the first three letters of the specific epithet (species) name. Table 6 contains a complete listing of species names. Three general groupings of species were evident. The first group

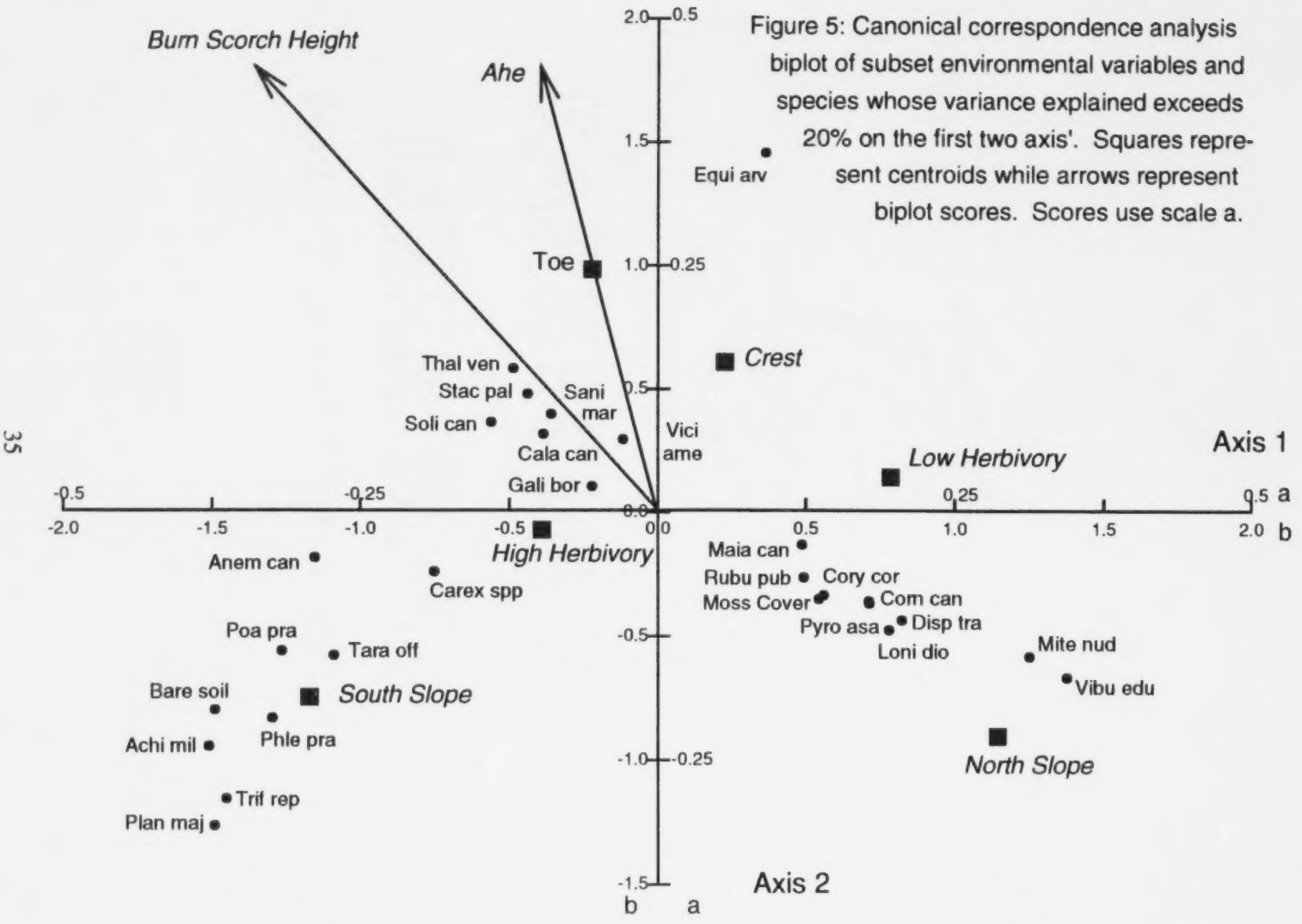


Figure 5: Canonical correspondence analysis biplot of subset environmental variables and species whose variance explained exceeds 20% on the first two axis'. Squares represent centroids while arrows represent biplot scores. Scores use scale a.

appeared near the ordinates of the south slope and high herbivory variables and included Taraxacum officinale (dandelion), Plantago major (plantain), Phleum pratense (timothy), Trifolium repens (white clover), and Poa pratensis. In addition, bare soil was positioned here. A second cluster of species was found near the north slope including Viburnum edule, Mitella nuda (bishop's cap), Pyrola asarifolia (pink wintergreen), Cornus canadensis (bunchberry), Maianthemum canadense (lily of the valley), and the cover of moss. A third general grouping of species was evident throughout the central portion of the biplot and includes the remaining native herbs which did not fall into either of the previous groups. These species are found away from the high herbivory and north slope variables. In general, the species found here are mostly tall forbs and grasses such as Solidago canadensis (Canada goldenrod), Sanicula marilandica (snakeroot), Thalictrum venulosum (meadow rue), and Calamagrostis canadensis.

5.2 Vegetative Response to Disturbance and Topographic Position

5.2.1 Overstory

The characteristics examined include live tree density, basal area, and canopy cover. Mean overstory stand characters and their significances are provided in Table 3. Average burn scorch heights by topographic position, taken from the stems of trees within the burned area, were 48, 63, 127 and 22 centimeters, for the toe, south facing, crest, and north facing positions, respectively.

Total live tree density was significantly lower inside the Park, where herbivory was higher (Table 3). When interspecific densities were examined, however, several discrepancies appeared. While the mean density of Populus tremuloides stems declined significantly from the other treatments (@ P=0.052), the density of Populus balsamifera, the other major tree species, did not differ between disturbances (Table 3). In addition, mature 'tree-like' forms of Amelanchier alnifolia, Prunus virginiana, and Prunus pensylvanica were found exclusively on the controls outside the Park, where they contributed substantially to total tree densities. They were found on seven, four, and two of the 12 control transects, respectively, and averaged 275, 233, and 58 stems/ha. Several other species including Betula papyrifera and Crataegus rotundifolia (hawthorn) were found in numbers too sparse to interpret.

Although total mean basal area was lower in the burned area, it did not differ significantly from either of the other two treatments. The reduction in overstory canopy cover inside the Park proved significant on the burned area only (Table 3).

The decreased stem frequencies inside the Park were most noticeable in those stem diameter classes under 20 cm (Figure 6). Mean comparisons revealed that the control differed from both the burned (P=0.018) and unburned (P=0.019) treatments. Stem frequencies under five centimeters diameter were almost nonexistent within the Park (Figure 6), indicating forest regeneration was poor in this area. Stands inside the Park were dominated by proportionately more larger stemmed trees.

Topographic position affected some of the overstory characters (Table 3). No

Table 3: Density, basal area, and canopy cover of the tree overstory by disturbance and topographic position.

	Total Tree Density : (#/ha)	Aspen Density: (#/ha)	Balsam Density: (#/ha)	Total Basal Area: (m^2/ha.)	Live Canopy Cover: (%)
Disturbance:	P = 0.065	P = 0.056	P = 0.228	P = 0.118	P = 0.030
Burned	646 b	467 b	179 a	16.4 a	40.7 b
Unburned	746 b	* 633 a b	71 a	27.1 a	60.9 a b
Control	2238 a	1475 a	117 a	30.1 a	75.8 a
Position:	P = 0.774	P = 0.528	P = 0.001	P = 0.002	P = 0.001
Toe	1211 a	806 a	378 a	29.1 a	64.2 a b
South	1072 a	745 a	6 b	15.1 b	39.5 c
Crest	1328 a	917 a	6 b	18.0 b	53.4 b c
North	1228 a	967 a	100 b	36.0 a	79.4 a
Pos. x Dist:	P = 0.004	P = 0.018	P = 0.338	P = 0.119	P = 0.001
Toe x Burned	1350 a	733 a b	615 a	30.5 a	60.1 a
Toe x Unburned	750 a	517 b	217 b	29.7 a	76.0 a
Toe x Control	1533 a	1167 a	300 b	27.1 a	56.5 a
South x Burned	117 b	117 b	0 a	2.1 b	5.4 b
South x Unburned	233 b	233 b	0 a	10.3 b	24.5 b
South x Control	2867 a	1883 a	17 a	32.8 a	88.7 a
Crest x Burned	367 b	367 b	0 a	7.8 a	20.6 b
Crest x Unburned	850 b	750 b	0 a	23.1 a	62.6 a
Crest x Control	2767 a	1633 a	17 a	23.0 a	77.1 a
North x Burned	750 b	650 a	100 a	25.3 b	76.8 a
North x Unburned	1150 a b	1033 a	67 a	45.3 a	80.7 a
North x Control	1783 a	1217 a	133 a	37.4 a b	80.9 a

Means represented by the same letter are not significantly different at P=0.05 using the Least Significant Difference test.
Interaction comparisons are between disturbances and within positions.
* Note: The unburned aspen density is significantly different from the control at P=0.052.

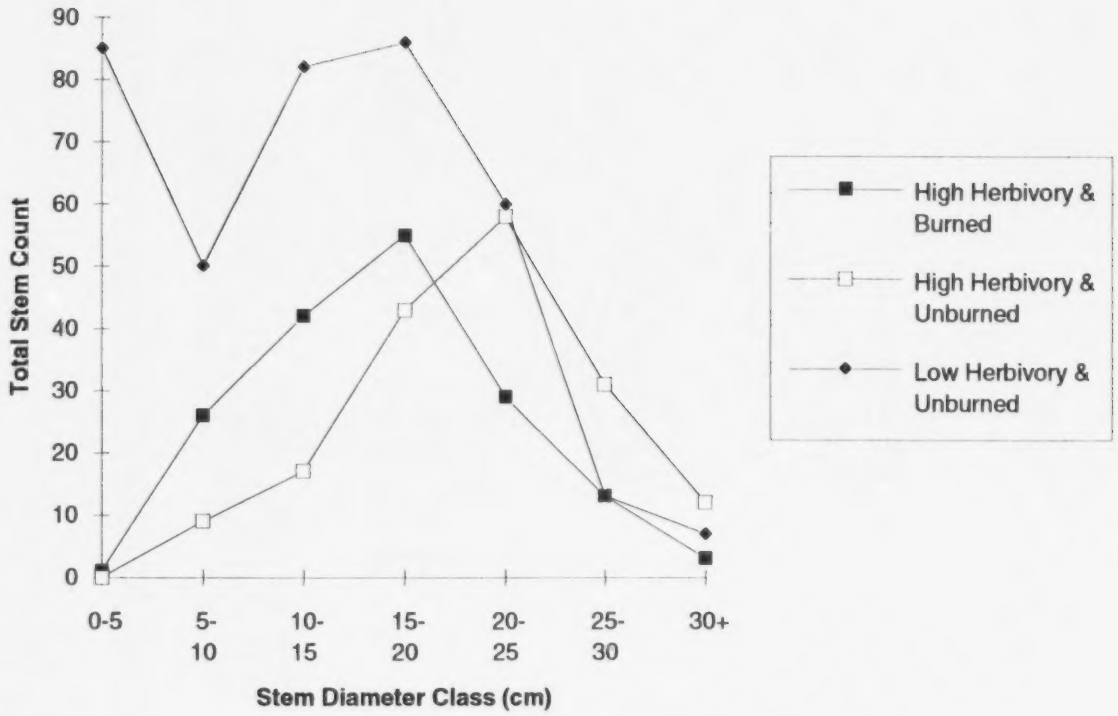


Figure 6: Stem frequencies by diameter class under various disturbances.

differences were apparent in total tree density or Populus tremuloides density. Only the density of Populus balsamifera and stand basal area varied significantly. The average Populus balsamifera density on toe slopes was significantly higher than on other topographic positions. A significant increase in total basal area was observed on both the toe and north slopes compared to the south and crest positions. Canopy cover varied considerably with the north slope showing the highest cover and the south slope the least (Table 3).

Topographic position affected stand structure inside and outside the Park with the highest stem frequencies at the north position evident in the larger diameter classes (> 15 cm) (Figures 7 and 8). Younger trees, represented by smaller stem diameter classes, had relatively low frequencies. North aspects inside and outside differed from one another only in the frequency of juvenile trees present (< 5 cm).

Stem frequency distributions within the remaining positions responded differently inside versus outside the Park. Toe slopes outside had relatively abundant numbers of small, medium, and large stems (Figure 8). Crests and south aspects in the same area were dominated by the small and medium diameter classes only. Inside the Park, the toe and crest positions also had tree densities peaking in the intermediate diameter classes (10-20 cm), although no small diameter regeneration was evident (Figure 7). South slopes at sites inside the Park had very few trees.

Total tree and Populus tremuloides densities displayed similar interactions between the disturbances and positions in the landscape (Table 3). The most significant declines in tree density inside the Park, occurred at the south facing and crest positions (Figure 9). Reductions in canopy cover were also evident at these sites, particularly on the south slope where a very significant decrease took place (Figure 10). While burning produced only a small additional reduction in stem density at the crest position inside the Park (Figure 9), a more important change was the significant decline in live canopy cover (Figure 10).

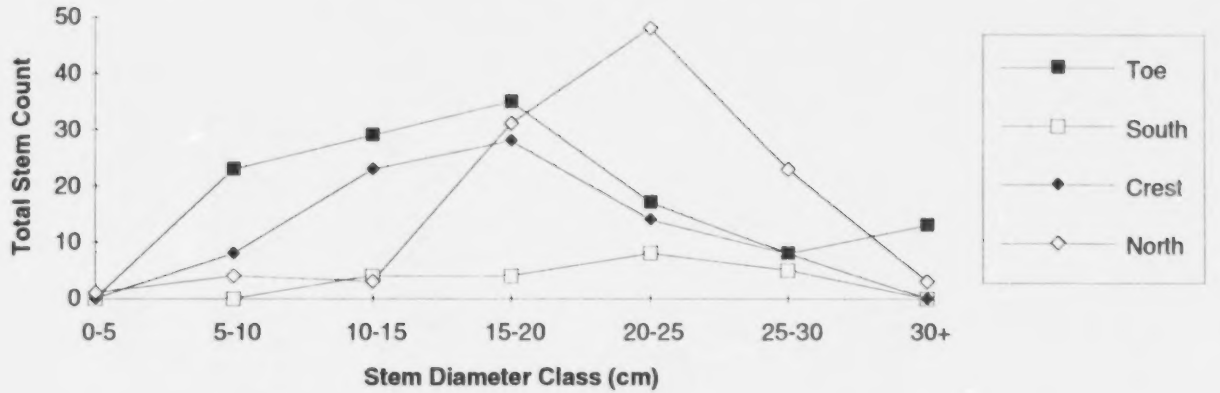


Figure 7: Stem frequencies by diameter class inside the Park.

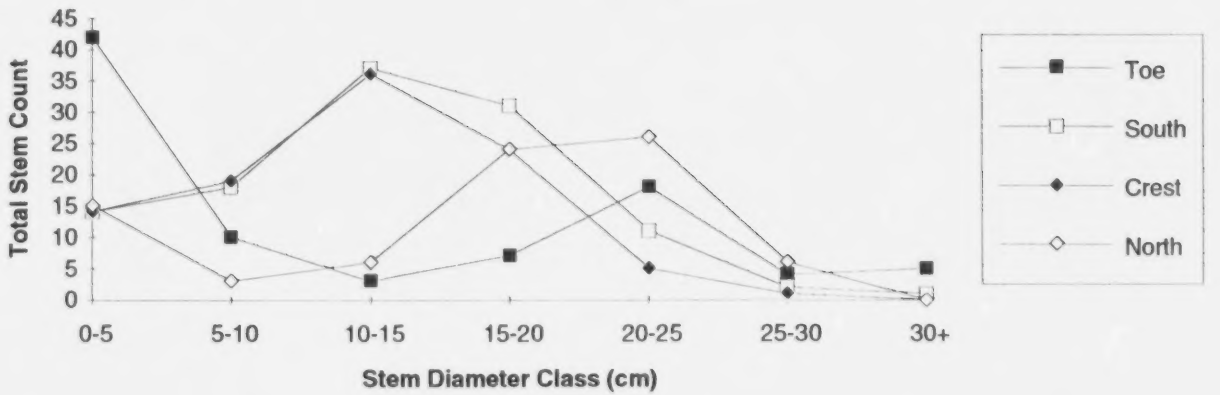


Figure 8: Stem frequencies by diameter class on the controls.

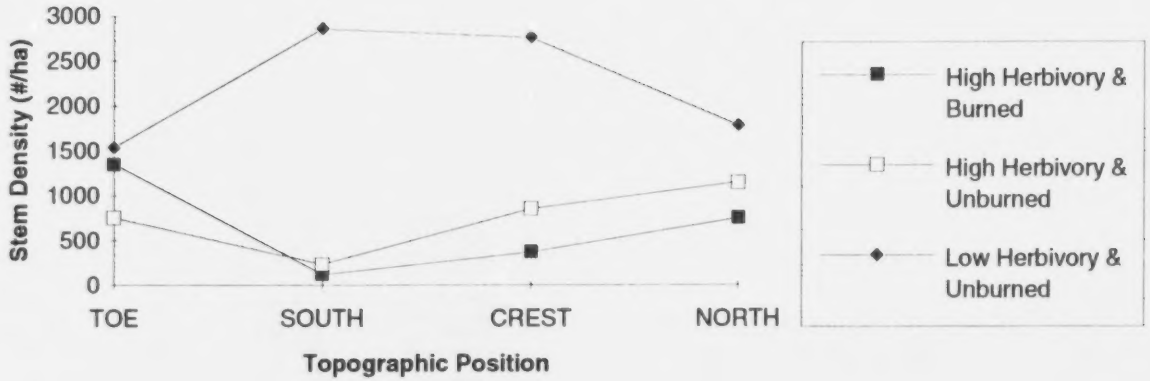


Figure 9: Total tree densities under various disturbances.

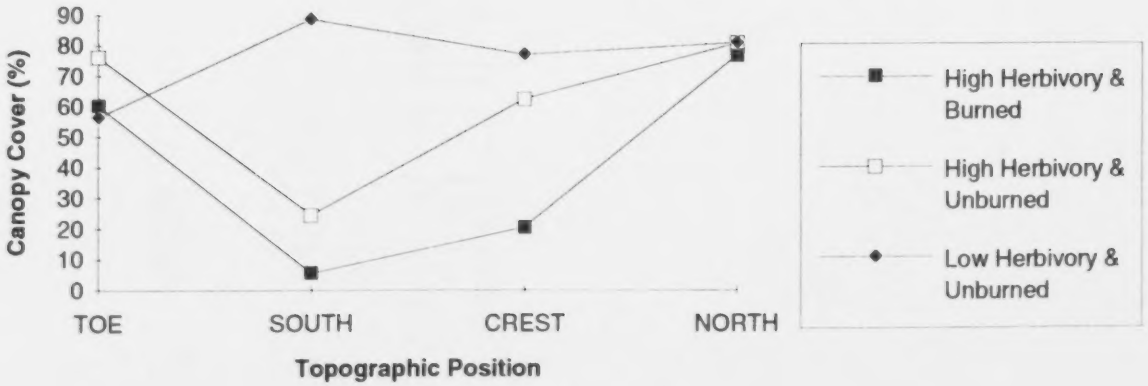


Figure 10: Canopy cover under various disturbances.

5.2.2 Understory Vegetation

The understory includes those plants found below the tree canopy. They form the lower strata of the community which are generally rich in shrub and herb species. Characteristics which are important include species diversity and structure of the shrub layer. Table 4 contains mean comparisons between the disturbances and positions for each understory characteristic.

5.2.2.1 Species Diversity

Herbivory and burning history had little impact on total diversity and species richness (Table 4). The invader diversity index, however, was significantly higher inside the Park, which is grazed more intensely. A further increase was observed on the unburned area, although this change was later shown by the interactions to be limited to the south slope position.

Total diversity and species richness were uniform across topographic positions with one exception (Table 4). Both characteristics were significantly higher on the toe slope compared to every other position.

Invader diversity was more variable between topographic positions (Table 4). South aspects had a significantly higher proportion of invaders than any other position. Toe slopes had an intermediate index, significantly higher than the crest and north, which had relatively few invaders.

Total species diversity was relatively unaffected by interactions with the only significant change being a decline on the unburned south slope (Table 4). Other interactions indicate that although the higher invader diversity occurring inside the Park took place on all positions, significant increases were limited to the south facing (both burned and unburned) and toe (unburned only) slopes (Figure 11). The largest difference among invader indices was evident on the south facing slope, with only a moderate increase at the toe position. A relatively small difference appeared at the crest, and even less at the north slope.

Table 4: Species diversity, species richness, shrub density, and shrub height index by disturbance and topographic position.

	Total Diversity Index :	Invader Diversity Index:	Species Richness: (#)	Shrub Density: (#/m^2)	Shrub Height Index: (cm)
Disturbance:	P = 0.812	P = 0.001	P = 0.335	P = 0.002	P = 0.001
Burned	2.85 a	0.18 b	36.6 a	18.6 a	54 b
Unburned	2.80 a	0.28 a	39.8 a	13.0 b	56 b
Control	2.79 a	0.04 c	37.4 a	10.7 b	108 a
Position:	P = 0.005	P = 0.001	P = 0.001	P = 0.065	P = 0.001
Toe	3.09 a	0.16 b	44.6 a	12.5 b	64 c
South	2.68 b	0.42 a	35.0 b	16.3 a	61 c
Crest	2.77 b	0.07 c	34.9 b	14.4 a b	77 b
North	2.71 b	0.01 c	37.3 b	13.3 b	88 a
Pos. x Dist:	P = 0.222	P = 0.001	P = 0.067	P = 0.123	P = 0.011
Toe x Burned	3.00 a	0.19 a b	39.7 a	16.7 a	47 b
Toe x Unburned	3.20 a	0.22 a	48.3 b	9.2 b	52 b
Toe x Control	3.08 a	0.08 b	45.7 b	11.7 b	93 a
South x Burned	2.87 a	0.45 b	35.0 a	23.6 a	41 b
South x Unburned	2.40 b	0.76 a	33.0 a	14.8 b	33 b
South x Control	2.77 a b	0.06 c	37.0 a	10.5 b	109 a
Crest x Burned	2.72 a	0.08 a	32.3 b	18.4 a	51 c
Crest x Unburned	2.84 a	0.13 a	40.3 a	14.7 a b	70 b
Crest x Control	2.75 a	0.01 a	32.0 b	10.2 b	109 a
North x Burned	2.80 a	0.01 a	39.3 a	16.0 a	76 b
North x Unburned	2.76 a	0.03 a	37.7 a	13.2 a b	69 b
North x Control	2.56 a	0.00 a	35.0 a	10.6 b	119 a

Means represented by the same letter are not significantly different at P=0.05 using the Least Significant Difference test.
Interaction comparisons are between disturbances and within positions.

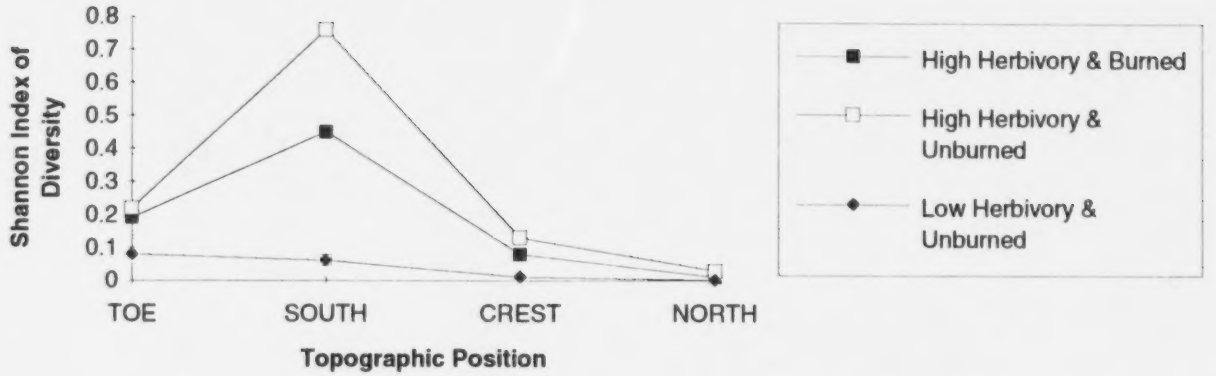


Figure 11: Invader species diversity under various disturbances.

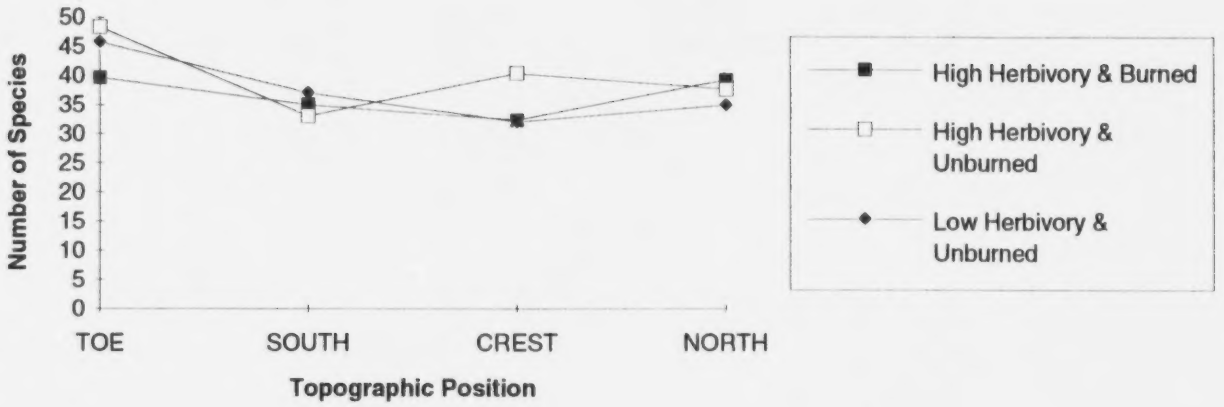


Figure 12: Species richness under various disturbances.

Species richness displayed few interactions, particularly at the north and south facing positions. A slight but significant increase was evident on the unburned crest (Figure 12). Richness was also higher on the unburned toe compared to the burned toe.

5.2.2.2 Shrub Layer

Shrubs in the study area were affected by both the disturbances and positions (Table 4). Total shrub densities were significantly higher on the burned area. To determine which shrub species were responding to burning, a stepwise regression was done between shrub density and tree burn scorch height using the densities of those individual shrub species which were found on at least half the burned transects. Of the seven eligible species, only Rubus idaeus entered the model at P=0.15 with an R^2=0.46. Investigation of the individual correlations between species stem density and burn scorch heights, however, revealed that two species had moderately positive responses and two negative. These were Rubus idaeus, Corylus cornuta, Amelanchier alnifolia, and Symphoricarpos occidentalis, with simple correlations of 0.68, 0.56, -0.41, and -0.30, respectively.

Shrub heights displayed the opposite response to densities, with significantly larger height indices found on the controls compared to the burned and unburned areas.

Topographic position also affected the shrub layer (Table 4). Densities were significantly higher on the south facing slopes than on the toe and north slopes. Height indices were significantly higher on the crest and north facing positions, particularly the latter. The lowest height index was found on the south aspect.

These differences are better explained by examining the interactions present between the disturbances and positions (Table 4). Although increased stem densities as a result of burning were found across all positions, significant increases were confined to the toe and south facing position (Figure 13). A second trend was also evident. On the control, shrub stem densities at three of the four positions tended to be lower than either of those within the Park.

Interactions within the height indices offered little new information (Figure 14). As expected, shrubs on the controls were taller at every position compared to those inside the

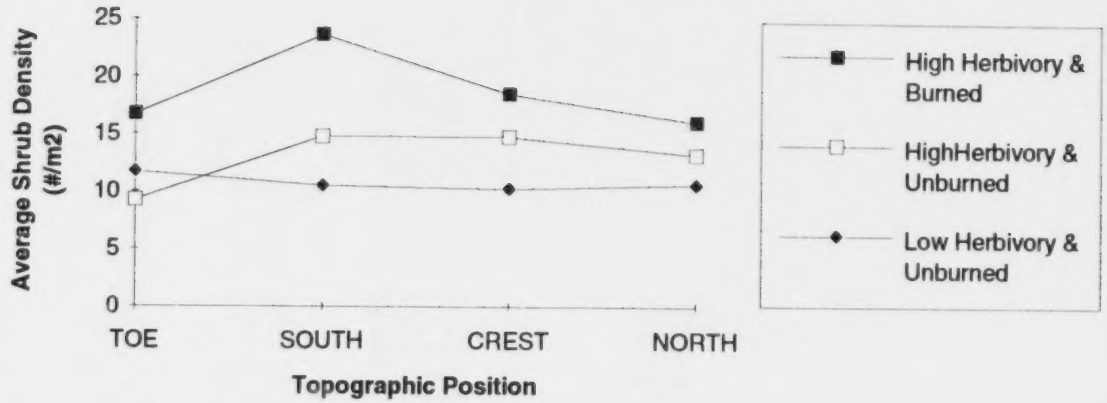


Figure 13: Total shrub stem densities under the various disturbances.

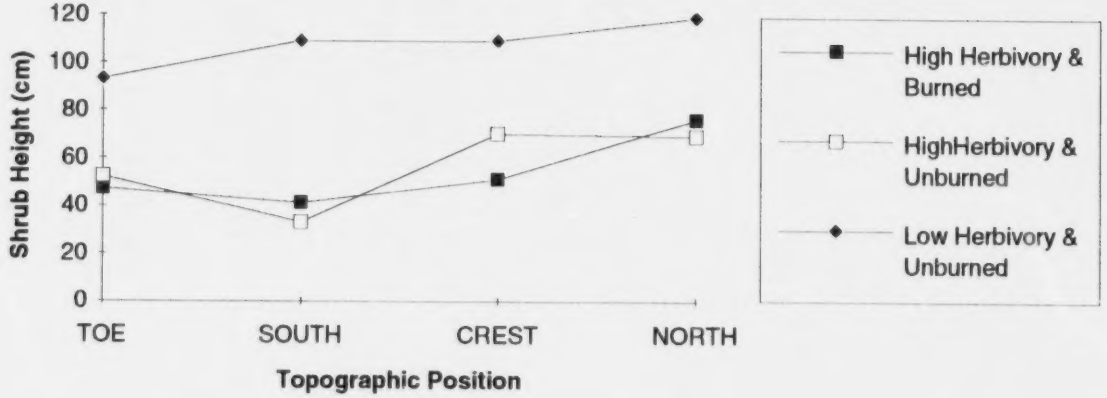


Figure 14: Shrub height indices under the various disturbances.

Park. An additional significant decrease in shrub heights, however, was observed at the crest position within the burned area.

5.2.3 Current Annual Production

Disturbance affected current annual above ground production in several ways (Table 5). Burning significantly increased grass, forb, and total current annual production (Figure 15). Although the unburned area of the Park experienced a general increase in grass and forb production compared to the control outside the Park, it did not differ significantly. In contrast to the herbs, both leaf and twig components were significantly higher on the control outside the Park, and had no overall response to burning (Table 5).

Topographic position had variable effects on annual production (Figure 15). Compared to the toe and crest positions, grass production was significantly higher on the south facing slopes and lower on the north facing slopes. Forbs were significantly lower on the north aspect only. Although twig production did not respond to topographic position, leaf production was significantly higher on the crest and north slope compared to the toe position. The large amount of leaf material produced on the crest was also significantly higher than on the south slope. Total production across topographic positions reflects a combination of herb and shrub growth in the landscape (Figure 15). The crest displayed the highest production and was significantly larger than both the toe and north slopes. Although the south facing slope was intermediate in annual growth, it remained significantly higher than the north slope.

The disturbances appeared to interact with the landscape positions in the annual production of individual biomass components (Table 5). The general increase in grass (Figure 16) and forb (Figure 17) production observed inside the Park proved significant only on the south, toe, and crest positions for the grass, forb, and forb components, respectively. The further increase in herb production evident on the burned area was more consistent among positions, but also limited to the toe, south facing, and crest positions. North slopes generally displayed little variation in grass and forb production, regardless of disturbance (Table 5).

While twig (Figure 18) and leaf (Figure 19) annual production were higher at all positions on the controls, the only significant increase was evident on the toe slope. Although the response in browse production following fire was relatively poor overall,

Table 5: Grass, forb, browse, and total current annual above ground production (kg/ha) by disturbance and topographic position.

	Grass :	Forb:	Shrub leaf:	Shrub twig:	Total:
Disturbance:	P = 0.001	P = 0.001	P = 0.005	P = 0.043	P = 0.006
Burned	595 a	808 a	519 b	140 b	2062 a
Unburned	305 b	525 b	544 b	145 b	1519 b
Control	85 b	392 b	847 a	273 a	1598 b
Position:	P = 0.001	P = 0.012	P = 0.017	P = 0.261	P = 0.007
Toe	304 b	660 a	492 c	160 a	1616 b
South	573 a	590 a	532 b c	174 a	1869 a b
Crest	356 b	647 a	808 a	221 a	2033 a
North	81 c	403 b	714 a b	189 a	1387 c
Pos. x Dist:	P = 0.015	P = 0.051	P = 0.049	P = 0.054	P = 0.123
Toe x Burned	559 a	966 a	258 b	85 b	1867 a
Toe x Unburned	213 b	662 b	384 b	115 b	1375 a
Toe x Control	141 b	352 c	835 a	280 a	1608 a
South x Burned	1013 a	829 a	629 a	191 a b	2680 a
South x Unburned	615 b	431 b	315 a	80 b	1440 b
South x Control	72 c	510 b	653 a	251 a	1446 b
Crest x Burned	693 a	984 a	440 b	99 b	2215 a
Crest x Unburned	276 b	633 b	848 a	250 a	2006 a
Crest x Control	100 b	324 c	1137 a	315 a	1876 a
North x Burned	98 a	455 a	748 a	185 a	1487 a
North x Unburned	116 a	372 a	631 a	135 a	1254 a
North x Control	28 a	383 a	763 a	247 a	1421 a

Means represented by the same letter are not significantly different at P=0.05 using the Least Significant Difference test.
Interaction comparisons are between disturbances and within positions.

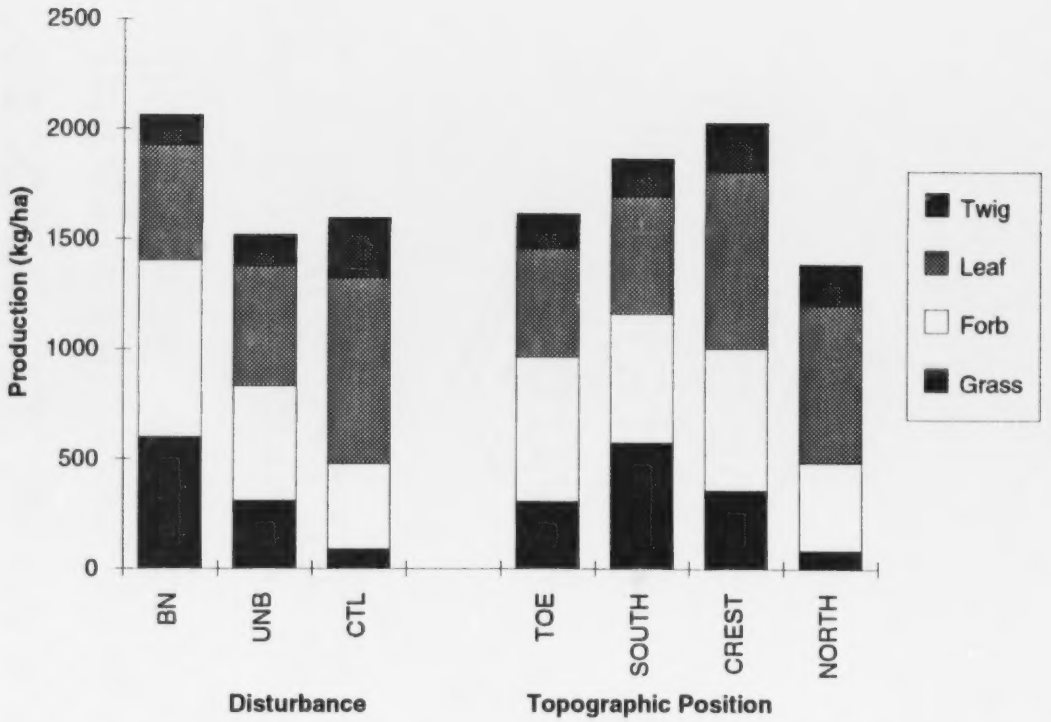


Figure 15: Composition of total current annual production by disturbance and position.

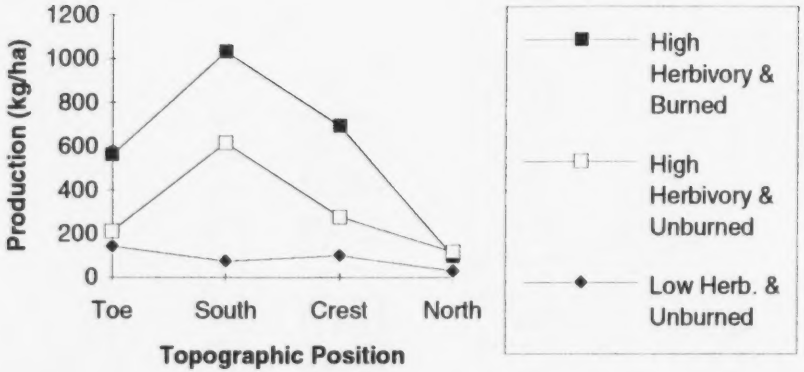


Figure 16: Grass current annual production.

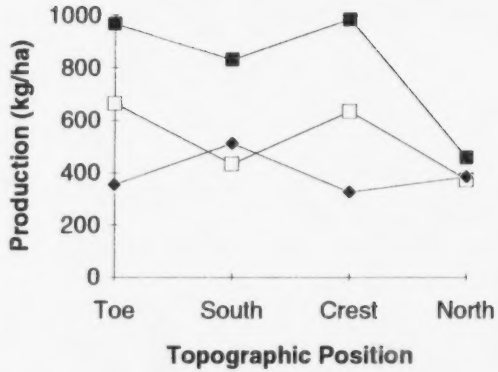


Figure 17: Forb current annual production.

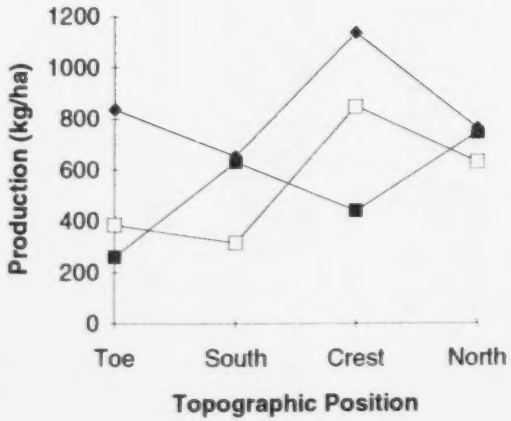


Figure 18: Twig current annual production.

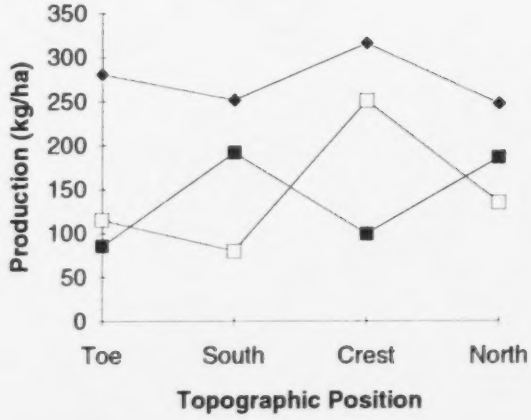


Figure 19: Leaf current annual production.

a significant decrease did occur in both shrubby components at the crest position within the burned area.

Total current annual production was relatively consistent across the various interactions (Figure 20). While total production was consistently higher throughout the burned area, the only significant increase took place on the burned south facing slope.

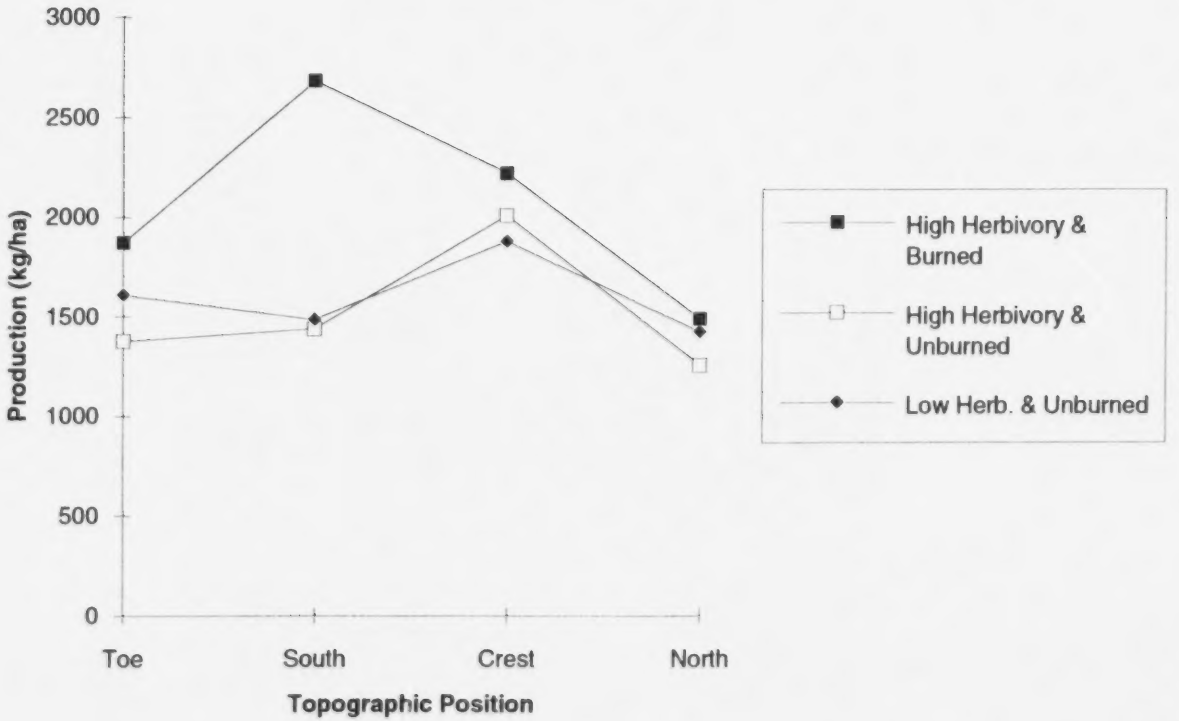


Figure 20: Total current annual above ground production.

5.3 Soils

Only two soil orders, Luvisolic and Gleysolic, were found on sites within the study area (Figure 21). Five Gleysols were found, all from the Orthic Luvic subgroup. Luvisols from two subgroups were found including 24 Orthic Gray and seven Gleyed Gray Luvisols.

The distribution of soil types between disturbances was relatively uniform (Figure 21). Variability does exist though, between topographic positions. The largest proportion of Gleysols and Gleyed Gray Luvisols were found on toe slopes. South aspects and crest positions were nearly exclusively Orthic Gray Luvisols. North slopes were predominantly Luvisols as well, although several exceptions occurred, including a Luvic Gleysol and two Gleyed Gray Luvisols.

Several additional observations were made. Although no Chernozems were found, several Luvisols had characteristics approaching those of Dark Gray Chernozems. Evidence of fire (ie. charcoal) appeared in 11 profiles including two, four, and five transects within the burned, unburned, and control areas, respectively. Generalized conceptual descriptions for each soil type are provided in Appendix IV.

Few conclusive statements could be made from the ANOVA of the soil characteristics, which included the thickness of the Ah, Ahe, and Ae horizons, as well as the pH and percent organic matter of the soil samples (Appendix V). It is, however, worth noting the increased pH at the toe slope relative to the north and crest positions, and the organic matter content, which was less in samples from the north facing slopes.

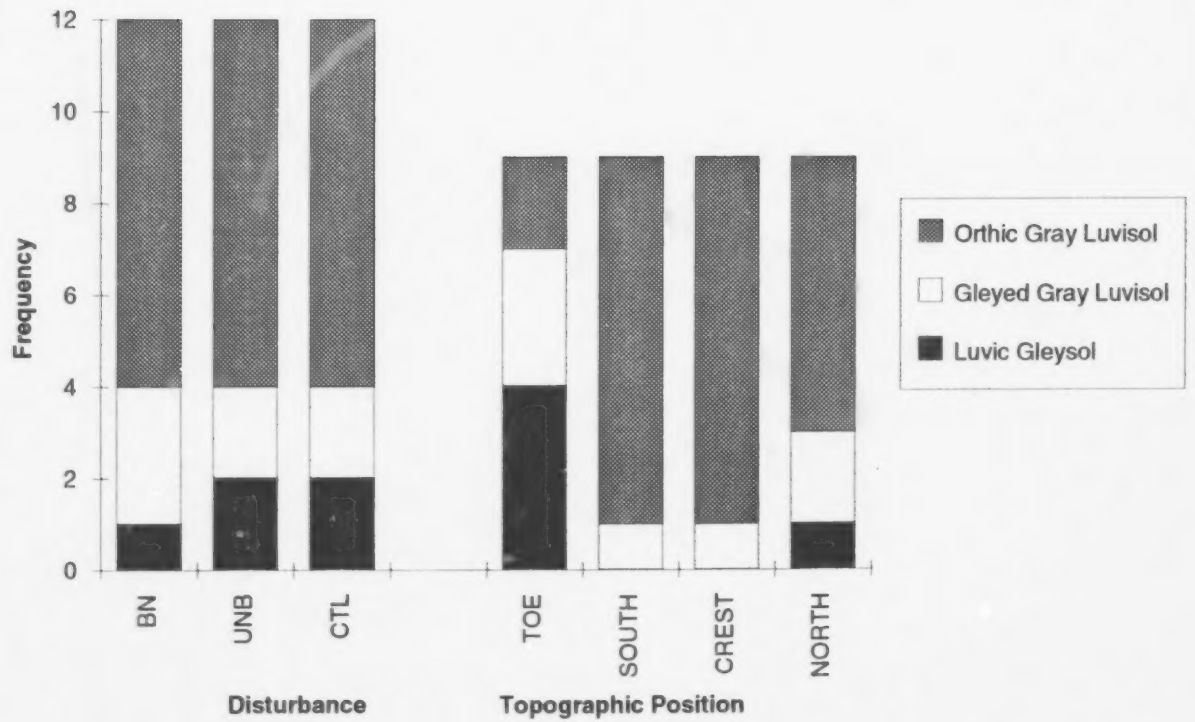


Figure 21: Frequency of soil types by disturbance and position.

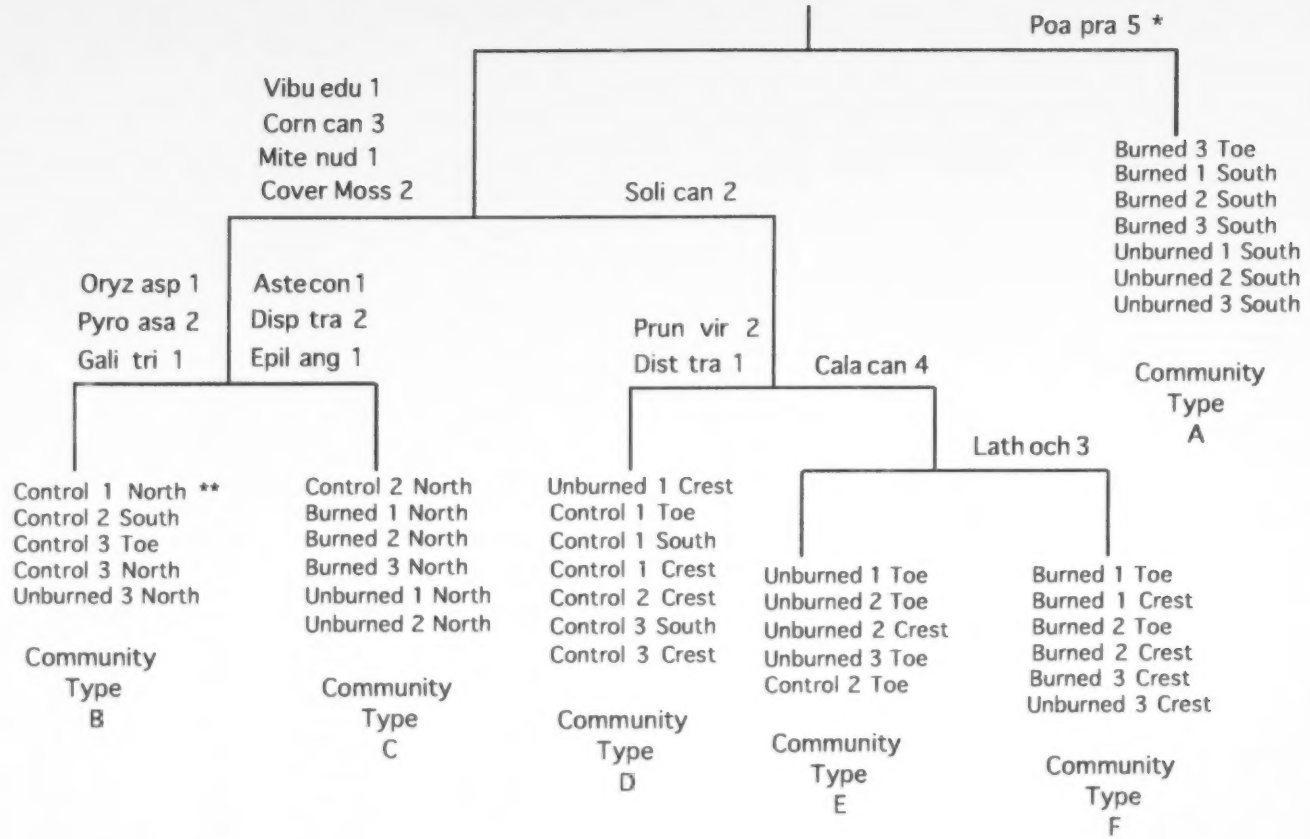
5.4 Classification of Plant Communities

Using TWINSPAN, six community types were identified from the inventory data and summarized in the form of a dendrogram (Figure 22). Transects classified to each type are shown at the bottom of the dendrogram. Indicator species and their order of importance are shown at each division where they were used to create each split in the dendrogram.

Table 6 contains a summary of the average canopy cover for the most abundant species in each of the six community types, labelled A through F. All indicator species and those identified on the biplots are included.

Figure 23 contains the ordination biplot of an indirect correspondence analysis (CA). The six groupings established by TWINSPAN have been roughly outlined and each sample site labelled with respect to the community type it represents. The ordination reveals that each TWINSPAN derived community type (Figure 22) generally occupies its own space within the biplot. Types E and F each contain a single outlier just above the x axis and to the left of the origin. Noticeable relationships include the close proximity of the south slope and high herbivory variables to community A, and the location of the north slope in relation to types B and C. Community F is generally situated in the direction of maximum variation in burn scorch height. A summary of the frequency of occurrence of each major environmental factor investigated, in relation to the derived TWINSPAN communities, is provided in Table 7.

A similar biplot to Figure 23 using the same layout shows all indicator species as detected by TWINSPAN along with the full set of vegetative characters analyzed passively in the same ordination (Figure 24). Interpretation of this biplot involves the identification of environmental factors, vegetative characters, and indicator species that relate more strongly to particular community types. Those variables located within or near a community generally relate to it the strongest. Not all factors will be easily interpreted, however, because some communities are the result of significant interactions among the surrounding variables.



* Note: Pseudospecies at each division are indicators as determined by TWINSPAN.

** Note: Sample sites falling in each community are listed by treatment, catena, and position.

Figure 22: Dendrogram of TWINSPAN analysis.

Table 6: Major species found in the communities of EINP.

Species:	Community Type ** A	B	C	D	E	F
			(% Cover)			
TREES:						
Populus spp.	19	77	78	76	70	43
SHRUBS:						
Amelanchier alnifolia	3	5	2	7	2	3
Corylus cornuta	9	60	49	31	14	20
Lonicera dioica	T *	2	2	T	T	T
Populus tremuloides	1	5	3	3	2	3
Prunus virginiana	2	2	1	7 *	1	1
Rosa spp.	7	7	10	22	11	11
Rubus idaeus	10	20	24	30	17	22
Symphoricarpos occidentalis	9	4	5	9	8	6
Viburnum edule	-	4 *	2 *	T	T	-
FORBS:						
Achillea millefolium	2	-	-	T	T	-
Apocynum androsaemifolium	T	T	T	7	1	3
Aralia nudicaulis	6	12	14	12	17	16
Aster ciliolatus	9	4	6	4	5	8
Aster conspicuous	2	1	6 *	8	1	4
Cornus canadensis	T	5 *	5 *	T	3	1
Disporum trachycarpum	-	2	3 *	2 *	1	T
Epilobium angustifolium	1	-	2 *	T	2	2
Equisetum arvense	-	T	T	1	2	T
Galium boreale	5	2	3	4	3	4
Galium triflorum	-	T *	T	T	1	-
Lathyrus ochroleucus	3	5	8	3	4	9 *
Lathyrus venosus	6	1	4	10	2	9
Maianthemum canadense	T	3	2	2	2	2
Mitella nuda	-	1 *	2 *	-	T	-

* Note: Denotes species which were identified as indicators by TWINSPAN.
** Note: A 'T' denotes species averaging less than 0.5% cover.

Table 6 (continued):

Species:	Community Type ** A	B	C	D	E	F
	(% Cover)					
Plantago major	1	-	-	-	T	-
Pyrola asarifolia	T	6 *	2	2	1	1
Rubus pubescens	1	15	9	3	7	6
Sanicula marilandica	2	1	1	1	5	4
Solidago canadensis	14	T	1	6 *	14 *	10*
Stachys palustris	1	-	T	T	T	1
Taraxacum officinale	5	T	T	1	1	T
Thalictrum venulosum	2	1	1	1	2	5
Trifolium repens	9	T	-	-	1	T
Vicia americana	6	3	5	3	4	9
GRASSES:						
Calamagrostis canadensis	21	6	11	4	19 *	33*
Carex spp.	4	3	T	1	2	2
Oryzopsis asperifolia	-	2 *	-	1	T	1
Phleum pratense	2	-	-	T	1	-
Poa pratensis	47 *	T	T	1	5	5
OTHER:						
Moss cover	2	7 *	4 *	1	4	T
Bare soil	6	-	-	-	T	1

* - Denotes species which were identified as indicators by TWINSPAN.
** - A 'T' denotes species averaging less than 0.5% cover.

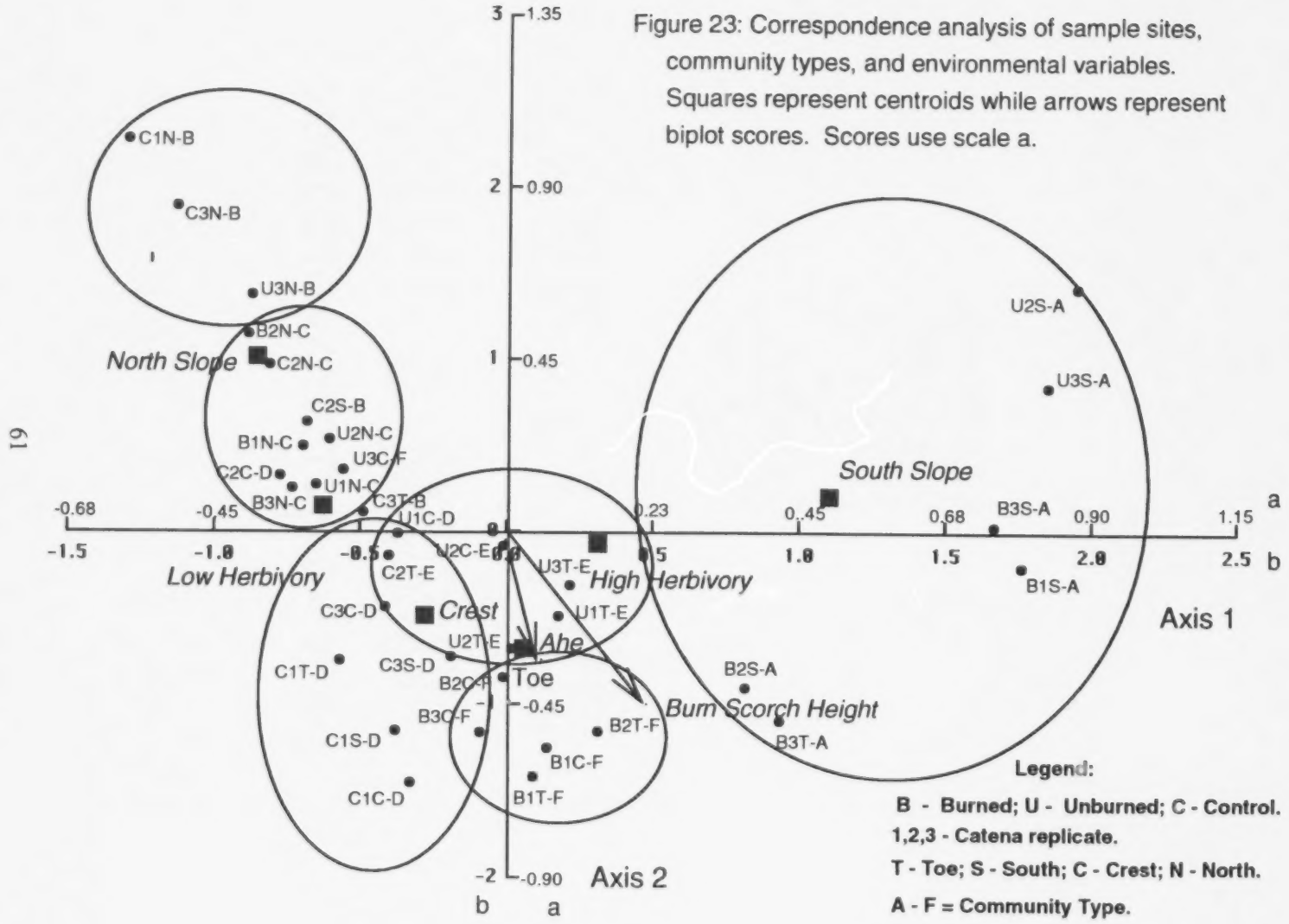


Figure 23: Correspondence analysis of sample sites, community types, and environmental variables. Squares represent centroids while arrows represent biplot scores. Scores use scale a.

Legend:

B - Burned; U - Unburned; C - Control.

1,2,3 - Catena replicate.

T - Toe; S - South; C - Crest; N - North.

A - F = Community Type.

Table 7: Summary of environmental factors within TWINSPAN community types.

Factor:	Community Type:					
	A	B	C	D	E	F
Fire:						
Burned	4	0	3	0	0	5 *
Unburned	3	5 *	3	7 *	5 *	1
Herbivory:						
High	7 *	1	5 *	1	4 *	6 *
Low	0	4 *	1	6 *	1	0
Position:						
Toe	1	1	0	1 *	4 *	2 *
South	6 *	1	0	2 *	0	0
Crest	0	0	0	4 *	1 *	4 *
North	0	3 *	6 *	0	0	0

Note: Community - factor combinations of importance are denoted by an '*'.

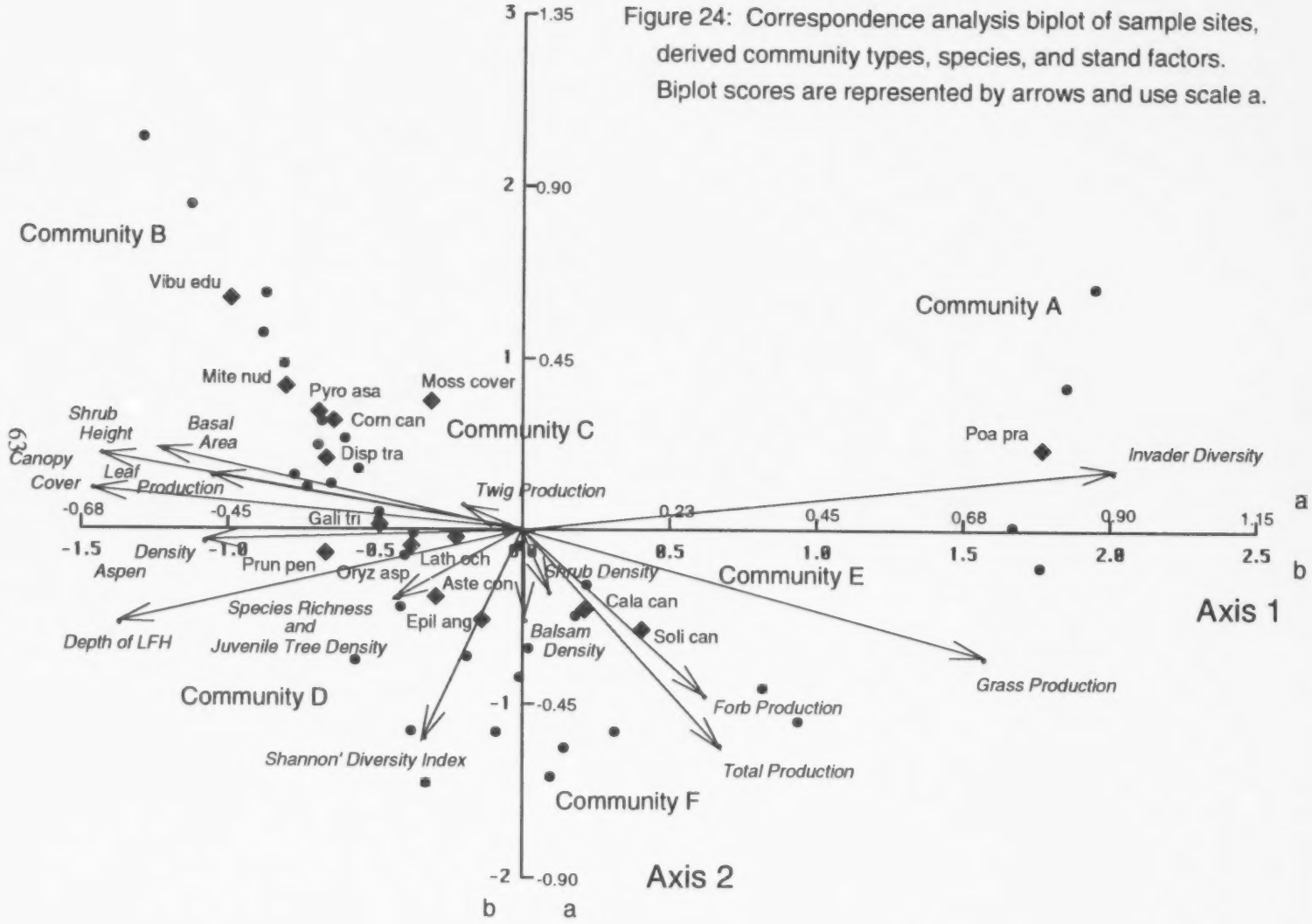


Figure 24: Correspondence analysis biplot of sample sites, derived community types, species, and stand factors. Biplot scores are represented by arrows and use scale a.

6. DISCUSSION

6.1 Community Classification

Upland community types within the study area were formed under several processes. Heavy foraging by ungulates, prescribed fire, and forest succession have all combined within the variable landscape to produce six relatively distinct community types. This classification differs from others for the same area (eg. Polster and Watson 1979; Hardy and Associates 1986; Blyth and Hudson 1987) in that it utilizes the composition of all species instead of relying solely on the overstory, and analyzes them using multivariate statistics. Classifications based on the overstory provide little insight into the role of environmental factors as they determine the type of plant communities found across the park's landscape. This is because the overstory composition can be relatively insensitive to soils and environment (Grigal and Arneman 1970). Other investigators, however, who used the understory, have also had difficulties relating environmental factors to a classification of plant communities (Polster and Watson 1979). Although the majority of the understory plant species in this study were found on all of the sample sites, certain indicator species and the structure of the shrub and herb layers varied sufficiently to produce the community types described. The use of multivariate analysis techniques and individual species compositions rather than the overstory alone, enabled this detailed classification to be established and interpreted ecologically.

Ecological classifications can be useful for establishing range succession models and illustrating relationships among community types. Traditional grazing models assume a linear relationship among communities with the management objective being to establish a stocking rate which produces a balance between grazing and succession. An alternative to this method is the state and transition model where vegetation dynamics can be described by a set of discrete states, with a series of transitional states in between (Westoby et al. 1989). Pathways from one state to another are interpreted as either opportunities or hazards, depending on the specific objectives of management. Although there are probably numerous other vegetative 'states' in EINP which are unaccounted for,

particularly because only limited areas of the Park were sampled, Figure 25 represents a theoretical example of a simplified state and transition model using the six derived communities. The model has two domains, with the second domain representative of prolonged intensive ungulate foraging. Shifts between domains may occur when a community in the first domain is altered by a disturbance of a particular magnitude, causing it to exceed its inherent level of resilience and thereby forcing it to enter the new domain (Noy-Meir and Walker 1986). While changes within a domain are reversible (double arrows) (Bosch and Kellner 1991), physical habitat changes accompanying the shift from one domain to another may make this transition irreversible (single arrow) (Bosch 1989), at least in the short term. For example, Naeth et al. (1990) associated both heavy grazing and early season grazing in central Alberta with increased compaction which produced higher soil bulk densities. Furthermore, the trampling and species compositional changes accompanying heavy grazing reduce the water holding capacity of soils (Naeth et al. 1991a).

Ungulate foraging and forest succession represent the major gradients within this model. Prescribed burning represents a more minor gradient and is currently found only within the first domain. Although topographic position may appear absent, its widespread affect remains evident in many community types as a result of it's interaction with the disturbances, and in it's impact on forest succession within the landscape. Potential transitions among forested types in the first domain are simple, based on moderate variability in foraging and forest succession, suggesting that these processes are probably reversible. A shifts to the second domain, however, marked by a large increase in the number of invaders from heavy grazing, may not be reversible. These species exhibit biological inertia (Acher and Smeins 1991), or an ability to compete with native species and maintain dominance in the community, even when grazing is removed. The time period for over which this continues, however, is often unknown.

Changes in the stocking levels and prescribed burning practices are the main tools available to resource managers to manipulate the EINP ecosystem and it's communities. Note that although community F is classed as a single state, the potential location of this community within the model is likely much broader because of the variable impact of

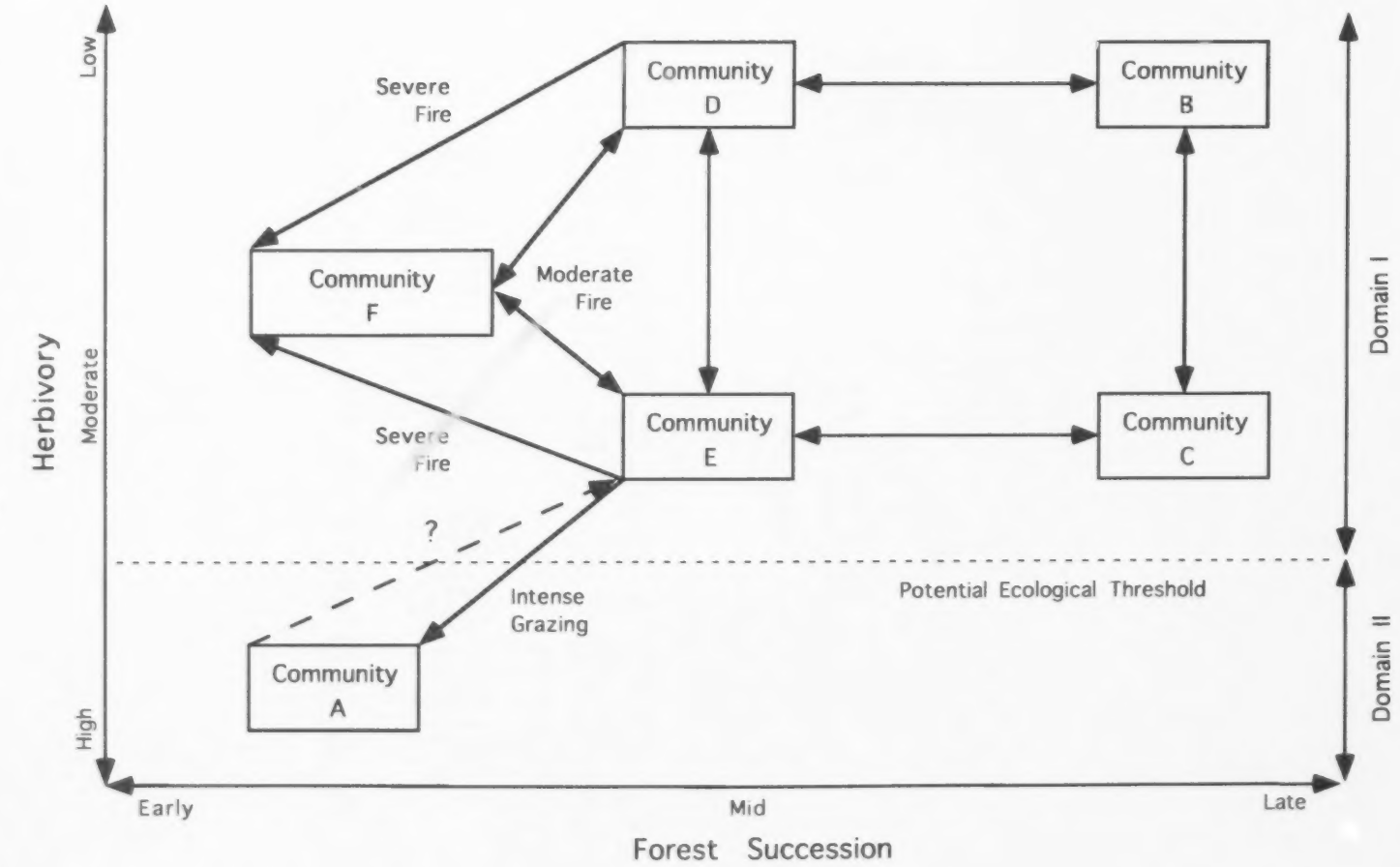
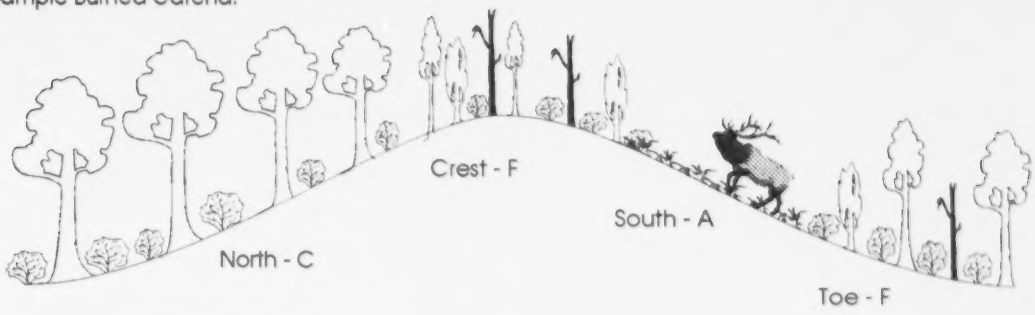


Figure 25: Potential state and transition model for Elk Island community types.

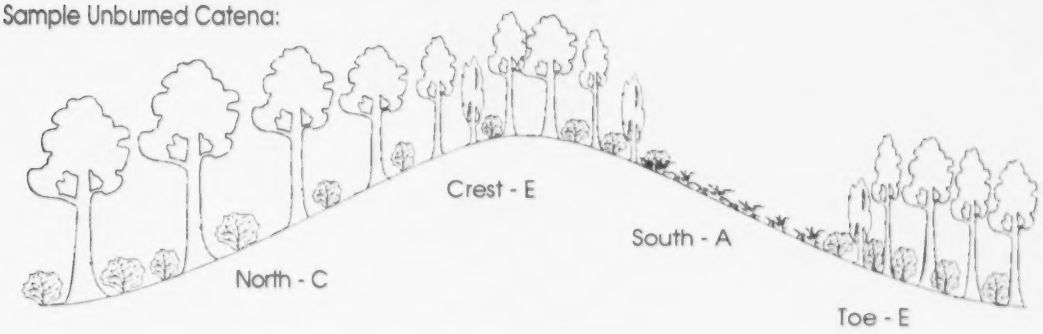
fire.

Following is a discussion of each community including where and why it is found in particular locations within the landscape and/or transition model, and how it compares to existing classifications. A summary of the locations of each community within the EINP landscape is presented in Figure 26. It is important to note that although many other community types probably exist in EINP, this classification provides a practical starting point.

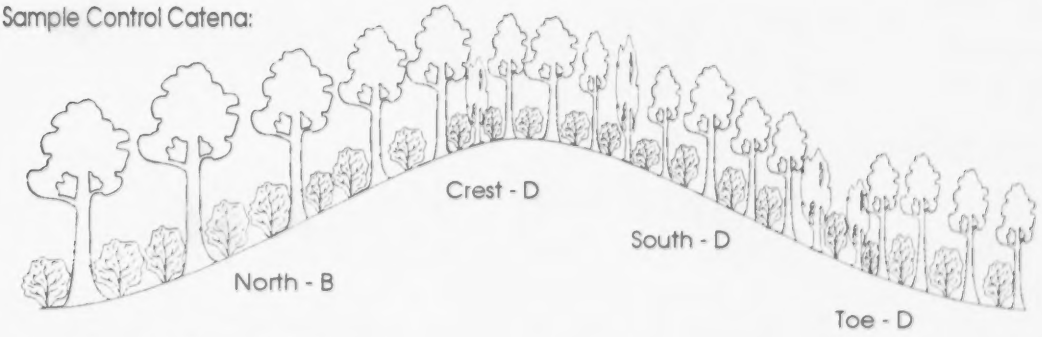
Sample Burned Catena:



Sample Unburned Catena:



Sample Control Catena:



Legend of Communities:

A - Poa pratensis - Calamagrosis canadensis

B - Populus tremuloides / Corylus cornuta / low herb

C - Populus tremuloides / Corylus cornuta / mixed herb

D - Populus tremuloides / tall mixed shrub / tall herb

E - Populus tremuloides / low mixed shrub / Calamagrostis canadensis

F - Populus tremuloides / low mixed shrub / Calamagrostis canadensis - Lathyrus ochroleucus

Figure 26: Sample layout of communities in the landscape under various disturbances.

6.1.1 Grasslands

Community A: (Populus tremuloides) / Poa pratensis / Calamagrostis canadensis

Community A was the only grassland documented. It appears to have occurred primarily because of sustained heavy ungulate foraging on south facing slopes inside the Park. These sites may have a partial live tree canopy. Any trees present constitute a minor part of the community. Although shrubs were present at moderate densities they were low in height and added little to total current annual production. The predominant differentiating characteristic of these sites was a high invader diversity index (Figure 24). This type was mostly found on south facing slopes inside the Park and represents sites similar to the grazing islands of Polster and Watson (1979) which are dominated by low shrubs and invader species (Plate 1). Grazing on these sites begins early in the spring and continues throughout the growing season. Although this community type can be found throughout most of the Park, it's distribution remains somewhat sporadic. The catenas examined in this study reflect this community quite strongly, in part because the areas sampled were generally larger hummocks which are more prone to heavy early season grazing.

Grazing tolerant species including Taraxacum officinale, Phleum pratense, Trifolium repens, and Poa pratensis, which was the primary indicator for this community (Figure 24), dominate these sites. The abundance of Poa pratensis on most grasslands throughout the Park is reflected in the classification by Hardy and Associates (1986) in which this species is dominant on two of the three grassland types classified. The abundance of invader grasses has resulted in these communities being high in grass production (Figure 24). Those native species which remained on sites with this community were usually sparse or were tolerant of intensive grazing. In addition, the average cover of bare soil was higher than on any other type (Table 6). This is indicative of excessive vegetation and litter removal which is often the result of heavy grazing (Naeth et al. 1991b). Communities most similar to this have been documented by Weatherill and Keith (1969), Bichlmaier (1985), Beckingham (1991), and Willoughby (1993a) in Alberta, and in the

Plate 1: Community Type A.

Plate 2: Community Type B.

intermountain region of the United States (Mueggler and Campbell 1982; Mueggler 1988).

6.1.2 Mature Stands

Communities B and C represent relatively mature Populus tremuloides forests similar to those of the boreal mixedwood forest. Although these two types were mainly found on north facing slopes, some sites from the south facing and toe positions outside the Park were included as well. The influence of fire appeared to be minimal, probably because of the lower fire intensities on these areas, particularly the north slopes. In general, the overstories were closed (> 75% cover), and dominated by older, larger stemmed trees. The proximity of canopy cover and basal area to types B and C can be seen in Figure 24. Characteristics of the shrub layer including its height index, twig production, and leaf production all tended to be higher as well (Figure 24). The overstory appears to be the major factor which separates communities B and C from the remaining forested types. Increased shading and competition has resulted in higher levels of Viburnum edule, Cornus canadensis, Mitella nuda, Pyrola asarifolia, and moss, all of which appeared as indicators (Figure 22) and were plotted near the ordination space of types B and C (Figure 24). These low growing species are adapted to the cooler, more moist, shaded conditions under the heavier tree canopy. The environmental conditions in the understory of communities B and C approximate those of the more elevated, cooler, and more moist, boreal mixedwood ecoregion (Strong 1992) to the north and west of EINP.

Although these two mature types differed relatively little in composition, as can be seen by their overlap in the ordination biplot (Figure 23), the structure of their understories were markedly dissimilar structurally because of differences in browsing. Polster and Watson (1979) also observed that herbivory has a larger impact on plant morphology than on community floristics. Types B and C have been classified separately in order to document these differences and facilitate their subsequent management.

Community B: Populus tremuloides / Corylus cornuta / low herb

The impact of herbivory on community B has been low. It represents a mature forest under minimal disturbance (Plate 2). Four of the five sites making up this community were from the lightly foraged controls located outside the Park. Although only three of the five were north facing, a more uniform tree cover across the catenas outside the Park enabled south facing and toe slopes to be included as well. Shrub height indices and canopy covers were very high because of the low impact of disturbances. Herbs found under the heavy shrub cover were relatively sparse and low growing. Exclusive indicator pseudospecies for this community included low growing herbs such as Oryzopsis asperifolia (indian ricegrass), Pyrola asarifolia, and Galium triflorum (sweet scented bedstraw).

A similar lack of tall herbs was observed in the understory of the Corylus cornuta communities documented by Kabzems et al. (1986) and Downing and Karpuk (1992). The latter investigators suggested the reduction was due to intense competition for light, moisture, and nutrients from the shrub layer. Although Downing and Karpuk (1992) documented two major Populus tremuloides / Corylus cornuta types over a relatively large area, all of the stands sampled in the EINP area had sufficient Corylus cornuta and Lathyrus ochroleucus (yellow peavine) to meet the requirements of their Populus tremuloides / Corylus cornuta - Rosa spp. / Lathyrus spp. vegetation type. Similarly, all forested stands sampled in this study correlated directly to the Populus tremuloides / Rosa - Rubus idaeus type in the classification of Environmental Management Associates Ltd. (1993). This would suggest that the classification derived from this study was either more detailed than those of the previous authors, or that Populus classifications are so specific that they can only be applied to the local areas from where they were originally derived. Prominent variation in the composition of the understory probably accounts for this specificity.

Community C: Populus tremuloides / Corylus cornuta / mixed herb

Community C was found on north facing slopes inside the Park. While also dominated by mature trees, the understory has been significantly altered by foraging. Corylus cornuta was again dominant in the shrub layer although it has taken on a lower growth form than in the previous type. The shorter shrub layer created by heavy browsing (Plate 3) enables several tall forb species to increase in abundance. The important tall forb indicators identified by TWINSPAN included Aster conspicuous (showy aster), Disporum trachycarpum (fairybells), and Epilobium angustifolium. Community C, together with community D, both were correlated to the aspen subtype of the Corylus - Rosa type of Polster and Watson (1979), and the Populus tremuloides / Corylus cornuta / Aralia nudicaulis type of Hardy and Associates (1986). The lack of further divisions within these classifications based on the understory suggest that they were more general. Although none of the communities found by Willoughby (1993a) had the same composition of dominant species as these mature Populus tremuloides types (particularly Corylus cornuta), communities B and C approximate his low and tall forb types, respectively.

6.1.3 Mid Successional Stands

The remaining three community types include stands from the toe, south facing, and crest positions only. These stands were younger and ecologically mid successional. Smaller stemmed trees were more prevalent in each of these types. Figure 24 reveals that these types, particularly type D, had the highest species richness and total stand diversity which is likely attributable to the intermediate amount of shading taking place. The changes in species composition and resulting classification suggest that both shade tolerant and intolerant species coexist in these communities.

Plate 3: Community Type C.

Plate 4: Community Type D.

Community D: Populus tremuloides / tall mixed shrub / tall herb

Community D was found almost exclusively on the lightly foraged control transects outside the Park (ie. 6 of 7). Although found on various topographic positions, it consisted mainly of crests and south facing slopes. This community was similar to type B in that it received only light foraging pressure. It differed however, in that it was composed of younger forests with less developed canopies (Plate 4). As a result, tall forbs such as Solidago canadensis, Aster conspicuous, and Lathyrus venosus (purple peavine) were common in the understory.

Community D also had a very prominent shrub layer with several dominant species. In addition to high levels of Corylus cornuta, Rubus idaeus, and Rosa spp., Prunus virginiana was identified as a key indicator species for this type.

Community E: Populus tremuloides / low mixed shrub / Calamagrostis canadensis

Community E was found on unburned sites inside the Park. Although it was predominantly found on toe slopes, this is likely coincidence and rather the result of two unburned crests being classified previously within other types. This community was very similar to type F. Both were dominated by the indicator herb, Calamagrostis canadensis (Figure 24, Plate 5). This species does well in conditions where shading is light. Low shading was the result of a reduction in tree and shrub canopies, which was associated with intensive ungulate use. This differentiates communities E and F from D, where light browsing failed to restrict the overall height and vigour of the shrub layer. Community E was most similar to the Populus tremuloides / Calamagrostis canadensis / low forb type of Willoughby (1993a).

Plate 5: Community Type E.

Plate 6: Community Type F.

Community F: Populus tremuloides / low mixed shrub / Calamagrostis canadensis - Lathyrus ochroleucus

Community type F was found mostly on crest and toe positions inside the Park and was closely associated with the intensity of burning (Plate 6). Both the crest and toe positions had relatively high fire intensities as determined by burn scorch height. In addition to the abundant levels of Calamagrostis canadensis, higher than normal levels of Lathyrus ochroleucus and Lathyrus venosus were present in this community.

Type F differed from community C, which also contained burned sites, in that the overstories found here were younger, more open, and the effects of fire more pronounced. The principle vegetative response appears to have been an increase in total production, particularly forbs (Figure 24).

6.2 Environment

The environmental factors which determined the type and composition of plant communities in and around EINP, were the disturbances and topographic positions. Soil types, horizon thicknesses, and textures explained only small amounts of the species variation among communities.

6.2.1 Geomorphology and Soils

In this study, topographic position had a pronounced effect on plant communities under each type of disturbance. These conclusions are similar to the findings of Milchunas et al. (1989) who concluded that catena position was more important than grazing and short term weather in affecting community structure within a semi-arid grassland. Topographic position influences vegetation by altering the site's microclimate (Hausenbuiller,1985). Willoughby (1986), Macyk et al. (1978), and Ayaad and Dix (1964), all found that available soil moisture was the main factor which varied with topographic position. This gradient was probably the major cause for the sharp vegetative changes evident across the landscape.

The most influential positions were the south facing and north facing slopes. These variables were selected first and third, respectively, in the forward regression and represent contrasting environments. South aspects generally receive more radiant energy resulting in higher soil temperatures (Pritchett 1979). This produces a general decrease in available moisture on the south compared to the north slopes (Macyk et al. 1978), which is further reflected in the plant species found at each location.

Although the toe and crest positions were less important they still explained a significant portion of the species composition data. Differences in drainage (Dix and Smeins 1967) and resulting moisture availability exist between these positions. Toe slopes are often associated with elevated water tables, as was evident by the increased occurrence of Gleysols at this position. Macyk et al. (1978) also classified soils from the toe position in central Alberta, as either Gleyed Luvisols or Gleysols depending on the

extent to which drainage was impeded.

There are several reasons why edaphic factors may be less important in the determination of plant communities. All of the sample sites examined in this study were collected from upland areas over a relatively small region of the Beaver Hills moraine. As a result, there were few major changes in the parent materials and soil textures. This in turn, is reflected in the high degree of homogeneity between plant communities, and the derived community types. The majority of plant species were found across all sites with only isolated indicator species (or pseudospecies) differing. Other studies such as those by Campbell (1986) and Jones et al. (1982) identify soil texture and parent material as key sources of environmental variation. These classifications, however, involve forests inventoried over vast regional areas containing major differentiation among the underlying soils and parent materials. The resulting classifications associated with these studies are also broad enough that they concentrate exclusively on differences among mature tree species. This approach would not be feasible in EINP because the sample sites are all dominated by Populus tremuloides, and the basic soil patterns the same.

Some soil characteristics are also limited in their importance and reliability as environmental gradients because of their delayed response to changes in vegetation. Soil characters, particularly those relating to subsurface horizons, are the result of soil development in response, in part, to the overlying vegetation over time (Spurr and Barnes 1980; Hausenbuiller 1985). Sudden retrogression in a plant community away from climax though, may leave the diagnostic soil characteristics lagging behind in a different state (Stoddart et al. 1975). For example, Dormaar and Lutwick (1966) found that after 85 years of occupation by Populus balsamifera, and despite detectable chemical changes, the soil profile did not display sufficient physical changes to reclassify the Chernozemic soil as a Luvisol. Soils can take long periods of time, up to thousands of years, to physically reflect the large scale successional changes that are occurring above them. In contrast, the disturbances, and changes in microclimate associated with variation in topographic position, affect vegetative growth directly. Therefore, these factors were detected more readily in vegetation sampling and analysis using multivariate techniques.

Changes in the soil chemical characteristics may also reflect vegetative change.

Scheffler (1976) found that soil phosphorus and potassium varied significantly with slope position in the aspen parkland, and Anderson and Bailey (1980) documented an increase in the phosphorus content of the Ah soil horizon following the use of prescribed fire. A different result may therefore have occurred in the ordination procedure if soil nutrients such as available nitrogen and phosphorus were examined instead. These soil characteristics change more readily across the landscape when the plant community inhabiting a site is altered, particularly by a disturbance such as fire (Daubenmire 1968a).

The thickness of the Ahe soil horizon was the last significant variable included within the model and is likely a result of being closely associated with the toe position (Figure 3). The thickness of this horizon will vary depending on the quality of the site for forb and grass growth, and its susceptibility to erosion. The migration of excess moisture down the slopes in hummocky terrain (Acton 1965) and favourable lighting conditions on the south facing toe slope promotes a relatively heavy herbaceous layer to form. The increased addition of organic root material eventually produces a thicker Ahe horizon. In addition, depressional areas in the landscape tend to accumulate topsoil as it erodes down from the surrounding slopes (Spurr and Barnes 1980) which in turn adds to the thickness of the Ahe horizon.

6.2.2 Disturbances

Both herbivory and prescribed fire had major effects on the plant communities in this study. High herbivory and burning were among the top four environmental variables selected in the forward regression. These disturbances have a direct impact on the vegetation through the defoliation and/or top killing of plants. As a result, prominent differences appeared between the communities investigated.

Of the two disturbances, herbivory appeared to be more important in altering the vegetation. It was selected before the burning variable and was more closely associated with the first axis. This could be attributed, however, to burning being included as a quantitative variable rather than a nominal one. Using nominal variables assumes that all replicates (or positions) have received the same treatment. Any interaction with position

would therefore not be reflected within the nominal herbivory variable. Because burn scorch heights were quantitative, variation in burn intensities throughout the landscape would be accurately reflected with some positions having lower fireline intensities than others.

The larger impact of herbivory could also be attributed to the time elapsed since each disturbance began. High ungulate densities within the study area have existed since shortly after its annexation into EINP in 1922. In contrast, prescribed burning has only recently become a major management tool being first put to use in 1979. Prior to that point, the last major fire in the area was in 1895. This is important since vegetative communities display some degree of resilience, or a natural ability to recover after environmental conditions change (Holling 1973). It is only after plants have had prolonged exposure to a particular environmental stress that they eventually die out and are replaced by others, producing a detectable compositional change. Therefore, it was possible that the communities in the burned area were in the early stages of ecological change and as a result, were more difficult to interpret.

It is also important to recognize that prescribed fire will rarely, if ever, replace wildfire in an ecosystem. The latter normally occurs at lower frequencies during very dry years (Wright 1974) and as a result are more effective at altering vegetation. Kjorlien (1977) notes that in the Beaver Hills, many wildfires which started out on the adjacent plains did not burn into the Park area unless conditions were ideal. Thus, those wildfires occurring would have had a major impact on the vegetation compared to prescribed fires, which are carried out as long as a certain basic prescription is met.

Another factor differentiating herbivory and fire is that intensive ungulate use has taken place consistently year after year, and over a full twelve month period, which includes the duration of the growing season. Continuous grazing, particularly during the growing season, is more likely to cause undesirable changes in species composition (Stoddart et al. 1975). In contrast, whether a burn is conducted and if so, its relative success, are both dependent on the weather and fuel conditions in that particular year at the time of ignition. Both the frequency and intensity of fire will affect the type and severity of changes in the plant community (Wright 1974; Vallentine 1980). In the last

10 years, the maximum number of burns on any one area has been four. In addition, because burning of Populus tremuloides forest is feasible only when the understory vegetation is dormant, cured, and providing an effective fuel supply (Jones and Debyle 1985), burning is unlikely to take place during the summer growing season when the vegetation is more susceptible to damage. Both an occasional burning frequency and dormant season burning, allows range plants to recover enabling communities to resist long term changes in composition. It is possible, however, that changes in the frequency, timing, and/or intensity of burns in the future, may alter the Park's plant communities more significantly.

6.3 Forest Overstory

Prescribed fire and ungulate foraging, often in combination with landscape position, have altered the forest overstory. The impact of herbivory on stand structure has been greater than that of fire alone. Generally, forest succession appears to be an unimpeded and stable process outside the Park while inside, succession is taking place without stand rejuvenation.

Higher tree densities on the controls could suggest that intensive browsing is decreasing tree densities inside the Park. This is particularly true for Amelanchier alnifolia, Prunus virginiana, Prunus pensylvanica, and Populus tremuloides, but not Populus balsamifera. The absence of mature forms of the first three species inside the Park could be caused by either their high palatability and the resulting preference for them among browsers (Bichlmaier 1985; Noste and Bushey 1987), or by an increased sensitivity to defoliation. Permanent range transects within the Park, which indicate that browse rates have not been unusually high for these species (Olson and Blyth 1986), suggest it may be the latter.

The indifferent response of Populus balsamifera to high herbivory is unusual given that this species is similar in crude protein, fibre and lignin content to Populus tremuloides (Bishoff 1981). Although no data were found comparing the presence of taste averting secondary compounds, aversion should not have been a factor given that Populus balsamifera had the highest relative contribution to the number of twigs browsed on range transects sampled from 1974 to 1981 (Olson and Blyth 1986), exceeding that of even Populus tremuloides. Therefore, possible explanations for the neutrality of this species are that the lower numbers of Populus balsamifera, found mostly on toe slopes, may have been insufficient to detect a significant change, that browsing pressures on these toe slopes were lower, that Populus balsamifera is more tolerant of intense browsing, or that less damage from insect pests may have enabled more of this species to survive.

The insect Malacosoma disstria (forest tent caterpillar) is an important forest pest in central Alberta. It prefers and generally has the greatest impact on, Populus tremuloides. Forests in the EINP area have experienced moderate to severe infestations during the late

80's and early 90's (Cerezke and Gates 1991). Although complete defoliation often occurs, Populus tremuloides is generally well adapted to this insect and causes little lasting damage (Peterson and Peterson 1992). It is not known however, what effect continuous annual defoliation by the tent caterpillar, compounded by other additional stresses such as drought, burning, or herbivory, may have on long term tree vigour and survival. It is therefore possible, that the additive stress of another defoliating agent on Populus tremuloides may have caused it to decline compared to Populus balsamifera.

The largest differences in tree density between the inside and outside of the Park were found in the small diameter classes. The abundance of small stemmed trees outside the Park and their uniform distribution among size classes indicated that overstory replacement and stand rejuvenation were actively taking place. Thus, in the absence of major disturbances, stable forest succession appears to become the dominant ecological process. It is important to recognize that although the area outside the Park is called the control, it does receive some foraging by native ungulates. Therefore, forest succession is occurring despite this inherent level of use.

Young Populus tremuloides stands normally contain high stem densities, with some exceeding 100,000 stems per hectare (Bella and De Franceschi 1980; Bartos et al. 1991). In part, this is due to the increase in soil temperature associated with forest removal at the time of disturbance (Maini and Horton 1966). As stands get older, disease, insects, browsing, snow breakage and the shading of suckers under intense competition results in self thinning (Debyle 1985). In addition, increased shading of the forest floor by this time results in cooler soil temperatures which reduces suckering. Removal or opening up of the overstory due to fire or herbivory, normally reverses this process.

Inside the Park, however, few young stems were becoming established. The lack of regeneration was particularly unusual, because many of these areas were unforested and should be prime sites for active encroachment from adjacent clones. Neither Populus tremuloides expansion nor stand rejuvenation appeared to be taking place, because of the intensive browsing of emerging suckers which evidently results in their death. Several examples of this have been documented including those of Milner (1977) and Gruell and Loope (1974) for wapiti, and Fitzgerald and Bailey (1984) for cattle. A possible reason

for this in EINP, where browsing is consistently heavy year round, is that sucker removal is more detrimental late in the growing season when stems are unable to replenish their carbohydrate reserves before the onset of winter dormancy (Fitzgerald and Hoddinnott 1983). Therefore, without a rest period from browsing, little survival of suckers is likely. The heavy use of Populus tremuloides in EINP extends beyond the sucker stage as well, with stems beyond the normal reach of ungulates often killed. Large numbers of trees in the 3 to 6 meter height range were observed to be broken off after the spring of 1992. Under deep snow conditions when most shrubs are inaccessible, moose will break Populus tremuloides stems up to 10 cm in diameter in order to obtain forage (Telfer and Cairns 1978). The resulting lack of regeneration inside the Park produces forest stands which are skewed in favour of the larger and older trees. It is possible that if forest succession continues and stocking rates are not reduced, these older treed stands will age and eventually die, thereby thinning out the overstory. Continued lack of recruitment may eventually result in the formation of semi-open shrublands or grasslands. This process will be aided by Populus tremuloides stand breakup which occurs when openings appear in the canopy, and the additional stress imposed on the trees by the new environment accelerates their susceptibility to insects and diseases (Peterson and Peterson 1992).

Prescribed burning also failed to increase the density of small diameter trees, despite being adapted to the effects of fire (Peterson and Peterson 1992). One explanation is that the lower burn intensities at the north and toe positions did insufficient damage to the parent trees to induce regeneration. Poor suckering has been observed under low intensity fires where few Populus tremuloides were killed (Brown and Debyle 1989). This same argument, however, cannot be made for the crest position where suckering was also low. Both field observations and recorded burn scorch heights indicate that fire intensities at this position were quite severe, with major tree kill occurring. Thus, abundant suckering should have taken place. The general lack of recruitment is probably due to continuous intensive ungulate browsing rather than poor quality prescribed fires. Basile (1979) found that wapiti utilized as much as 44% of the current annual growth in Populus tremuloides stands three years after burning.

Poor stand rejuvenation may also be caused by the overall reduction in the proportion

of forested land within the burned area. This, combined with the attractiveness of browsing shrubby regrowth, would result in increased foraging within the remaining stands by the same ungulate populations. Thus, while burning may encourage suckering in general, it will also accentuate aspen control by reducing the effective area of forest cover and concentrating ungulate activity. Debyle (1979) noted that fire can only be used to regenerate Populus tremuloides stands if the area can be protected from browsing wapiti. Debyle (1985) also suggested that if several species of large ungulates are simultaneously using these forests as winter range, the impact will be even more severe and longer lasting. This is a close approximation to the situation in EINP.

The vegetative history of the Park contributes to the formation of the current forest stands within the study area. Paleoecological evidence suggests that the amount of tree cover occurring in the EINP area over the last century has been the highest levels experienced in the last 12 000 years (Vance 1979). Wildfire has long been a major factor in forming and maintaining the vegetation in the Beaver Hills. A large fire in 1895 removed much of the extensive forest cover present at that time (Kjorlien 1977). Therefore, what ratio of grassland to forest is modal for this region of the parkland is difficult to determine and remains speculative. It is worth noting that the recent historical evidence documenting an abundance of forest was supported in this study by the consistent finding of Luvisolic soils instead of Chernozems. Their dominance indicates that in the past, the Park's uplands must have been inhabited by deciduous forested vegetation for extended periods. The Luvisolic soils found on the grassy south facing slopes inside the Park, many of which have remained unforested since the Park's establishment, indicate that these areas also must have been forested, albeit well in advance of settlement of the area and creation of the Park. The exact time period over which this occurred, however, remains unknown, particularly because the specific rates of conversion from Chernozems to Luvisols are unknown in the region.

Aerial photographs taken shortly after 1922 reveal that many of the south facing slopes and crests were open grasslands or semi-open shrublands. Other areas such as the north and toe slopes had localized tree cover, presumably because of the reduced impact of the 1895 fire and favourable tree regrowth at these moister positions. Creation of the

Park marked the beginning of a period when wildfires were largely suppressed allowing forest succession to accelerate throughout the Beaver Hills. The result was that nearly all of the areas outside the Park became forested. As a consequence, the south aspects and crest positions in this area had intermediate or mid-successional stand structures while north and toe slopes were late successional stands. North slopes, which had the most advanced tree cover when fire suppression began, appeared to be the most mature.

Inside the Park, however, sustained intensive browsing on many south facing slopes after 1922 prevented trees from becoming established. Many of these sites have remained as open shrublands and grasslands. South facing aspects such as these are also the least favourable for Populus tremuloides growth making establishment additionally difficult (Scheffler 1976). Those areas which had larger trees present in 1922, particularly the north slopes, continued to develop and mature because they were well beyond the stage of being directly damaged by herbivores. Some forest development and stand expansion would have occurred in the Park's early years on the toe and crest positions where young trees were either already present or were encroaching from the adjacent forested areas (ie. the north). Those areas which did not have trees extending out of the reach of ungulates when moderate and high stocking rates were reached in the late 20's and early 30's, probably remained largely unforested. Blyth and Hudson (1987) documented an excerpt and accompanying photo from a statement by the park superintendent in 1937 where he noted that browsing was so great that whole areas of 160 acres to one square mile were relatively denuded of foliage. Stocking levels in the mid 30's were several times higher than at any other time (Blyth and Hudson 1987) and would have minimized the recruitment of Populus spp. during this period.

Additional events which may have helped release trees on the toe and crest positions took place in 1928-29, 1935-36, and again in 1959-60, when sizable reductions in bison populations were undertaken through slaughters. The brief time periods needed for populations to resurge may have enabled some of the young trees at these positions to reach heights beyond being susceptible to browsing. This may explain why the toe and crest positions inside the Park are now mid-successional forests, compared to the north slopes which remain late successional.

North slopes in general were dominated by larger stemmed trees indicative of older, relatively mature overstories. These mature forests probably account for the well developed Luvisolic soils found under them, as well as their lower organic matter content in the Ahe horizon. These stands, including those on the controls outside the Park, have fewer of the younger stems due to the size and vigour of the older trees. It is likely that these forests are more similar to the deciduous forest types documented by Corns and Annas (1986) in the boreal mixedwood ecoregion. This is further supported by the work of Nicholson (1993), who concluded that many of the depressional wetlands scattered throughout the Park are essentially outliers of the boreal mixedwood forest, with edaphic factors such as elevation, topographic position, and hydrology being more important causal factors than climate itself. This indicates that the north slopes, which are often contiguous to these depressions, probably represent microclimate conditions in between those of the riparian wetlands and those found on the dryer, more exposed, crest and south facing slopes. Another important consideration is that if forest succession on the south facing and crest positions outside the Park continues in the absence of a disturbance, these sites may approach a successional stage more similar to that of the north facing stands, depending on the degree of microclimate alteration in the understory by the Populus tremuloides canopy.

In comparison to herbivory, the resumption of burning inside the Park in the late 1970's resulted in several relatively minor changes in the forest canopy. Only Populus tremuloides densities decreased on the burned area. This species is distributed throughout the landscape making it more susceptible to an effective prescribed burn. Populus balsamifera was more abundant on the toe slopes where more moist conditions predominate. The moderate burn intensities found there, coupled with the thicker bark which this species possesses, may also have limited damage.

On a landscape scale, the most prominent effect of burning was the decrease in live canopy cover at the crest position. Intense burning, as evidenced by the extreme burn scorch heights, killed many of the trees at this location. Drier conditions, an abundance of fine and medium fuels, and increased wind speeds could all have contributed to the more severe fire intensities. Total tree densities were not reduced significantly at the

crest position, only because of the variation in the responses among catenas. Two of the three crests which were burned were totally denuded of live tree cover. In contrast, the third was burned less severely with the result that few of the trees were killed. These differences reflect how the repetition of prescribed burning and variable nature of fire in the landscape can impose very different treatments on each catena and transect. The low and moderate burn intensities observed on the north and toe slopes, respectively, were not severe enough to kill the larger stemmed trees found at these positions in the landscape (Quintilio et al. 1991). It appears that unless burning is done under highly favourable conditions, little of the tree canopy may be damaged at these topographic positions. Therefore, prescribed burning of even large areas, may ultimately affect only a portion of the landscape and total tree cover.

6.4 Understory Response

6.4.1 Species Diversity

Wilson and Keddy (1988) found that although disturbances may cause a variety of changes in species abundances, these changes may not be appropriately reflected by variation among general plant community characters. This appears to be the case in EINP, where species richness and total diversity reacted indifferently to the various disturbances. Despite the neutral response in these factors, changes in species composition did occur, as was evident by the higher proportion of total diversity consisting of non-native invader species inside the Park. The rich variety and uniformly distributed populations of native species found on the lightly foraged controls, have been replaced to varying degrees by invaders within the Park. Intense ungulate foraging has contributed to this change because many introduced species are adapted to withstand heavy grazing (Looman 1983; O'Connor 1991). Non native invader species are often low in growth form, highly rhizomatous, and therefore tolerant of heavy grazing. This process of species replacement is based on competitive exclusion whereby changes in environmental stress (ie. grazing) cause the removal of some species, thereby allowing those species which are tolerant of the new environmental conditions, to invade (Grime 1973a).

The similarity in total diversity between the heavily foraged Park and lightly utilized control is unusual considering that year long heavy grazing normally reduces diversity (Waser and Price 1981). A possible explanation is that because maximum species diversity is associated with intermediate levels of an environmental factor (Grime 1973b; Connell 1978), these two treatments may represent opposite sides of the bell shaped diversity curve along the foraging gradient. Therefore, increased foraging outside the Park could possibly increase its diversity by decreasing the ability of community dominants (ie. shrubs) to competitively exclude other species (Quinn and Robinson 1987). In turn, reduced foraging inside the Park may increase diversity by removing the competitive edge the non-native invaders currently hold, particularly in those parts of the

landscape where they dominate (ie. south slopes). It should also be noted that not all south facing slopes inside the Park are dominated by invaders to this degree. Many other south aspects exist which are smaller, have less relief, and have a greater portion of forest cover. These areas are only moderately affected by intensive grazing.

The increase in invader species inside the Park is particularly evident on the south facing slopes. These 'grazing islands' have unique vegetation and were the result of heavy grazing during the snow free period of the year. Ungulates use these areas to a greater extent because of their snow loss during the winter months and early green up in the spring. Grazing herbivores are attracted to these sites and congregate on them because of the ease with which they can obtain forage. Their palatable regrowth in late spring and early summer is then periodically regrazed, keeping the vegetation short and in poor vigour for extended periods. The general lack of upland grasslands inside the Park causes the two most abundant herbivores, wapiti and bison, to both utilize these select sites. This grazing pattern has continued in an intensive seasonal and yearly pattern creating significant changes in species composition on many of the south aspects inside the Park.

Positions other than the south facing slope were less likely to experience these heavy levels of use and have fewer invaders. Other positions were largely forested and able to trap considerably more snowfall. Partial shading of the understory limits premature snow loss and green up. Herbaceous species in these areas are unlikely to be grazed until early to mid summer after the main vegetation flush has begun. By that time, the growth of herbs and supply of forage would be large enough that utilization rates would remain relatively light until senescence begins in the fall. Given the above factors, the north slope, with the most well developed forest and shrub canopy, the greatest snow accumulation and least snow loss through the winter, and the least growth of herbs, had the smallest invader index. Little intensive grazing occurred there.

A further increase in invader species was found on the unburned south facing slope compared to the same position on the burned area. This could indicate that burning suppresses invaders. Although Stickney (1986) found exotics to be the most characteristic species which disappeared following a wildfire in Northern Idaho, the relatively small

amount of fuel on many of the south aspects in EINP and their early green up makes this explanation somewhat unlikely. Opportunities for burning under heavily grazed Populus tremuloides stands are reduced and even negated, because of the poor fuel complex available (Brown and Simmerman 1986).

Another, more likely explanation for the above difference in diversity, is that variation exists within ungulate foraging patterns throughout the Park. Cairnes (1976) found that wapiti used only one fifth of the Park during the winter months. Thus, if the unburned south slopes are part of their preferred wintering area, they will receive heavy use by wapiti at this time. Large wapiti herds have been observed on the unburned south facing slopes in March and may be a major reason that the vegetation found there is short and consists predominantly of invader species. The burned south facing slopes also receive heavy summer use, but may be subject to less early spring grazing, enabling a more even mixture of native and invader forbs and grasses to occur.

Although some evidence exists which indicates that burning decreases overall species diversity after a single burn (Collins and Barber 1985; Wilson and Shay 1990), other work suggests that herb richness is actually increased by annual burning (Anderson and Bailey 1980). No detectable response, however, was evident in this study. A possible explanation is that because burning took place at least two growing seasons previous to sampling, retrogression towards the original vegetation may already be taking place. In addition, because wildfire was quite common in the parkland, many of the species found there are probably adapted to fire indicating that drastic shifts in diversity are less unlikely. An alternative explanation, however, is that the effect of burning may have been masked by high herbivory within the Park. That is, while burning may have increased the number of species, intensive grazing may have simultaneously removed many others. It may therefore be, that if only one disturbance (ie. fire) had been investigated in the EINP study, the effect of burning on diversity may have been different.

Other minor changes in species richness and diversity were evident among the landscape positions as a result of burning. A decrease in species richness on the burned crest and burned toe positions within the Park suggested that some species may have been reduced or eliminated as a result of burning. Those species affected would be intolerant

of fire because of their growth habit. Generally, plants having concealed growing points below the mineral surface are less likely to experience long term damage or death (Brown and Debyle 1989). Those fires with high enough intensities, however, were more likely to penetrate deeper into the LFH layer and damage the resident plant crowns. The crest and toe positions experienced the two highest fire intensities, respectively, as indicated by the burn scorch heights. Species remaining on these sites were either adapted to withstand intense fires or were able to recolonize the area immediately following the disturbance (Stickney 1986; Bradley et al. 1992). Stickney (1986) found that despite an overall increase in the number of species from 103 to 120 ten years after a burn, the net increase of 17 was actually made up of the loss of 19 and a gain of 36 species. Thus, the identity of those species which changed, rather than the number of species (ie. species richness), may provide more insight into the true ecological response of burned areas.

Of all the topographic positions, only the toe slope affected total diversity and species richness. The increase in these attributes was probably caused by the favourable moisture conditions present. These sites remain very moist without extensive flooding. This enables wetland adapted species to extend up from the depressional meadows or sloughs and dryland species to extend down from the south aspect. The result is a richer mosaic of species inhabiting the toe slopes. Maximum species diversity was once again associated with intermediate levels of an environmental factor, in this case moisture and drainage.

6.4.2 Herb Layer

Most herbaceous species found during the inventory were uniformly distributed across the disturbances and topographic positions. This reflects both the wide tolerance of these species to variation in their environment and the homogeneity of most environmental factors among sample sites. Although there were several species documented in this study that were abundant, these were not always important from an ecological perspective. For example, Aralia nudicaulis was found throughout most of the study sites, but similar to the findings of Hardy and Associates (1986), its abundance meant no strong ecological

interpretations could be made concerning its presence. Instead, several noteworthy indicator species and species groupings were documented by the ordination biplots (Figures 23 and 24) and TWINSPAN dendrogram (Figure 22).

A group of non native invader species was closely associated with the south facing slopes inside the Park. Of these, Poa pratensis was predominant. This highly competitive, early growing, cool season species is grazing tolerant (Vallentine 1980). Although many invader species are unpalatable and maintain prolific seed production even under heavy grazing (O'Connor 1991), this species is palatable and nutritious when kept in a vegetative state, and increases under this regime because of its abundant creeping rhizomes (Looman 1983). The increases of this species on the south slopes inside the Park may also be due to intermediate nitrogen enrichment (Wilson and Tilman 1991), associated with increased mineralization as a result of intensive, localized grazing (Crawley 1983; Brisk and Heitschmidt 1991). Another plant which occurs concurrently with Poa pratensis, is Taraxacum officinale. This species is also an early growing, highly competitive, non-native invader (Looman 1983). It should be noted that the dominant native grass once found in the northern portion of the parkland, Festuca scabrella (Coupland 1950), was not present in any community, including the sole grassland type. This trend towards 'local extinction' of dominant native species is characteristic of changes in the temporal and spatial patterns of grazing in human influenced systems (O'Connor 1991). Increases in the intensity and duration of grazing in EINP have probably lead to the disappearance of Festuca scabrella.

The second group of species includes those low growing herbs which favour more moist, partly shaded growing conditions. Included in this group were Oryzopsis asperifolia, Rubus pubescens (dewberry), Cornus canadensis, Mitella nuda, Pyrola asarifolia, and the cover of moss. These species were closely associated with the north aspects where heavier forest canopies and poorer solar reception occur. Many of these species are widespread and common throughout the boreal forest of northern and western Alberta under mature deciduous, mixedwood, and coniferous forests (Corns and Annas 1986; Willoughby 1993a). This further supports the theory that the north facing slopes in EINP were more representative of boreal forest conditions. The other positions

investigated were probably too warm, too dry, and too exposed for any of these species to dominate. In addition, the north facing slopes experience lower fire intensities. Bradley et al. (1992) list Galium triflorum, Oryzopsis spp., and Pyrola spp. among those that are susceptible to fire-kill. All three of these appeared as indicators for community types found on north facing slopes suggesting they may also be more abundant there as a refuge from exposure to severe fire.

The lack of tall forbs in each of the above two groups, indicates that tall forbs were favoured by either lower foraging intensities or younger successional forests. Willoughby (1993a) suggested that an absence of tall forbs meant grazing by cattle was replacing tall forbs with grazing tolerant low ones, or that forest succession was advancing to a point where tall forbs could no longer compete in the understory. Both of these theories appear to have validity in EINP.

Tall forbs no longer dominate on the heavily grazed south facing slopes inside the Park. The continued presence of tall forbs across the remaining positions inside the Park might suggest that herbivory limits the development of tall forbs only when it occurs at a high intensity. In addition, the contrary may also be true, with moderate browsing of the shrub layer stimulating tall forb development, by removing part of the competitive shrub canopy. The uninhibited shrub growth outside the Park, particularly on the north aspects suppresses tall forb species. Although not as prominent, forest succession also appeared to be a factor, particularly when stands become very mature as was evident on the north facing slopes.

Other individual species which had notable responses included Solidago canadensis, Calamagrostis canadensis, and Lathyrus ochroleucus. Solidago canadensis was abundant on all areas except the heavily forested north slopes. This suggests that this species will not tolerate extensive shading. Although Calamagrostis canadensis was found on nearly all sites, it was particularly abundant inside the Park on aspects other than the north. Work by Leiffers and Stadt (1993) indicates that an overstory canopy transmitting only 20-30% of light should provide sufficient shade to suppress this grass. They further found that mature Populus tremuloides stands transmit as little as 20% of total light. Thus, suppression of this grass may be occurring on north facing slopes. In contrast, the

higher Calamagrostis canadensis levels on all other positions inside the Park may be due to its release from the mature canopy, brought on by the reduction in overstory tree density and canopy cover associated with burning and increased herbivory. Lathyrus ochroleucus was the only herb to display a large detectable positive response to fire. This is similar to the large increase in canopy cover, from 0 to 30.8%, documented by Quintilio et al. (1991) following repeated spring fires in central Alberta. Anderson and Bailey (1979) also documented a favourable response to fire among various legume species and suggested it may be due to fire's ability to break their seed dormancy in the soil. Lathyrus ochroleucus is important because it is abundant, productive, and nutritious in deciduous forests, although remaining susceptible to overutilization (Beckingham 1991). The poor response of other species to fire is somewhat surprising because there are numerous species, including Epilobium angustifolium, which are known to respond very positively to fire (Looman 1983; Stickney 1986; Bradley et al. 1992). The impact of high herbivory immediately following burning, may have limited the growth of these fire adapted forbs. It is also possible that increases may have taken place immediately following each fire, but that they were relatively short lived (ie. one season). The composition of the understory normally reverts back to pre-burn conditions, at a rate which is dependent on the intensity of the fire itself (Bartos and Mueggler 1981). Understanding these rates of reversion are important when managing any area using fire.

6.4.3 Shrub Layer

Extensive browsing has maintained shrubs in a shorter growth form throughout the Park. Bishoff (1981) found browse consumption in the forests of EINP to be approximately twice that of current annual production, indicating that much of the browse consumed was two and three year old wood. This intensity of use has resulted in short, thick stemmed shrubs, with numerous leaders at the top which are regularly removed by ungulates producing a distinct browse line. In complete contrast, and despite light browsing, shrubs outside the Park possess a tall and bushy growth form.

The tallest shrubs were consistently on the north facing slopes. These aspects are

often the site of deep snow accumulations during the winter months. Deep snow affects the selection of forage by ungulates (Telfer 1978) by reducing the accessibility and subsequent browsing in the area.

Further reductions in shrub heights at the burned crest position were caused by the higher fire intensities as suggested by burn scorch heights. Fire intensity is a direct result of the net heat of combustion, the amount of fuel consumed, and the fire's rate of advance (Alexander 1982). Intense fires at the crest position would arise as a result of the site's reduced duff moisture, brought about by increased exposure, an abundance of both fine and medium fuels, and a greater accessibility of wind to accelerate fire spread. Fires at the crest were therefore more likely to top kill shrubs. Most of the shrubs found at this position were the result of regrowth from the forest floor. Many of the shrubs present at the other landscape positions were better able to withstand the lower fire intensities, and remain within the community. For example, north slopes had the lowest fire intensities, probably because of the sparse amount of fine fuels and the high duff moisture which would occur as a result of poor solar reception.

Stem densities had the opposite response of shrub heights, being higher inside the Park. The moderate increase in shrub density may be caused by several factors, acting either independently, or in combination. Many shrub species respond physiologically to defoliation by increasing the number of stems produced (Stoddart et al. 1975; Crawley 1983). Abundant basal resprouting and/or growth from rhizomes often accounts for part of this increase. It is important to recognize that much of the browsing in EINP occurs during the winter months when alternate forages are unavailable. Certain shrubs can withstand heavy utilization year after year, providing the majority of use is during this dormant period (Stoddart et al. 1975). In comparison to the results in EINP, work by Bailey et al. (1990) showed that heavy grazing by cattle during the growing season actually decreased the density of all woody species. This indicates that the current level of use inside the Park, particularly during the critical summer period, may not be as heavy as the prominent browse line suggests. Instead, the larger proportion of browsing probably occurs during the winter.

Further examination of the response of stem density among topographic positions

indicates that no increase occurred on the north facing slope. Therefore, another factor which may be responsible is the more open forest and shrub canopies found inside the Park. Increased light reception and higher soil temperatures at the forest floor may directly stimulate sprouting, as occurs with Populus tremuloides (Schier 1976). The north slopes inside the Park have retained prominent overstories and are logistically less likely to experience these increases in soil temperature, thereby minimizing the potential for resprouting.

The most dramatic increases in stem density inside the Park were apparent on the burned area. Increased densities across all topographic positions indicate that fires of all intensities were able to induce sprouting among shrubs. This response was far greater than the moderate increase observed on the unburned areas inside the Park. The favourable response to fire was not unexpected because numerous shrubs have been documented to respond favourably to fire (Bradley et al. 1992). The similar response of shrub stem densities among positions was explained by Johnston (1981). The latter simulated various burning intensities using fuel loadings and found that burn intensity affected the rate of recovery of Corylus cornuta and Rubus idaeus sprouts, rather that the actual number of stems produced. While fire reduces the cover and therefore, vigour, of shrubs, increases in stem density may still occur (Anderson and Bailey 1980).

It is important to note that the increased densities caused by burning were not consistent among species. Although both Rubus idaeus and Corylus cornuta were correlated with an increase, only the former produced a significant response in the regression model. This may be because while both species increase as a result of basal resprouting, Rubus idaeus also regenerates in large part from seed (Johnston 1981). The positive correlations observed here were similar to the results of other studies involving Rubus idaeus (Foote 1976; Anderson and Bailey 1979) and Corylus cornuta (Buckman 1964; Perala 1974; Ohmann and Grigal 1979). The more significant response of Rubus idaeus was somewhat unexpected, however, because Johnston (1981) concluded that this species was actually more susceptible to damage from fire than Corylus cornuta, primarily because of the relatively shallow depth of the Rubus idaeus root crowns. It is possible, however, that Corylus cornuta is less fire resistant when exposed to repeated fires over

relatively short intervals, as was done here. Another explanation could be that at the specific postburn time period when the data were collected, this species may still have been increasing while Rubus idaeus was peaking in density. Ohmann and Grigal (1979) found that the latter increases rapidly and then declines after fire, while Corylus cornuta takes longer periods to increase.

Whereas most shrubs showed no correlation to burning, other species displayed a negative relationship including Amelanchier alnifolia and Symphoricarpos occidentalis. Despite the tolerance of Amelanchier alnifolia to fire (Noste and Bushey 1987; Bradley et al. 1992) and the positive response documented by Anderson and Bailey (1980), this species decreased in stem density. The reduction observed here may be caused by preferential selective browsing of the regrowth of this palatable species. Although Symphoricarpos occidentalis has been found to rapidly increase following a single fire (Anderson and Bailey 1979), Anderson and Bailey (1980) documented a decline under a multiple burning regime. A decrease was also found by Bartos and Mueggler (1981). The unpalatable nature of Symphoricarpos occidentalis compared to other major browse species (Fitzgerald et al. 1986), indicates that heavy browsing was probably not the major reason for its decline. Instead, repeated exposure to burning, particularly while these shrubs were weakened and still recovering, may have caused irreparable damage. Determining the specific response of vegetation to fire is generally difficult because many factors influence post-burn vegetation including the pre-fire vegetation, species adaptations, environmental conditions, and chance (Brown and Debyle 1989).

Although individual species responses varied little, Viburnum edule did display a strong preference for the heavier forest canopies found on north aspects, regardless of disturbance. This species was closely associated with the group of low lying herbs, and is abundant throughout the boreal mixedwood forest types (Corns and Annas 1986), where it was found in both seral (aspen) and climax (spruce) communities. Despite adding little in total cover or production, this species remains potentially important because resource managers can identify sites high in Viburnum edule as mature, late successional, Populus tremuloides stands.

6.5 Forage Production

Current annual growth of the various vegetative components was influenced by both the disturbances and topographic positions. The higher production of grasses, forbs, and total biomass on most positions inside the Park compared to the lightly foraged controls, was probably caused by the reduction in shrub heights and tree canopy caused by years of intensive browsing. Reduced yields in the undergrowth of Populus tremuloides stands has been attributed to intense root competition which reduced soil moisture (Ellison and Houston 1958). Shrubs also compete with forbs and grasses for space, nutrients, moisture, and light (Spurr and Barnes 1980). A reduction in shrub competition would allow forb and grass production to increase. North aspects inside the Park did not experience as large a decrease in shrub and tree cover, and as a result, no herb production increase was evident. A major reason for the changes in production may have been from the shifts among dominant species. For example, increased levels of Poa pratensis and Calamagrostis canadensis inside the Park probably accounted for the higher grass production, while an increased abundance of tall forbs increased forb production. Maximum grass production was evident on the south facing slopes inside the Park where altogether few trees and shrubs were found.

The additional increase in herb production within the burned area inside the Park is unlike the decrease found by Anderson and Bailey (1980) after annual burning, but is similar to that found by other investigators after occasional fire (Harniss and Murray 1973; Bartos and Mueggler 1981; Brown and Debyle 1989). The former discrepancy may be caused by differences in fire intensities, the postburn growing conditions, or most likely, the frequency of fire. Frequent fire is more likely to damage plants and decrease their annual growth. The observed increase could be attributed to several factors including a further decrease in competition from the shrub and forest overstories. An indirect response is also possible through increased soil temperatures and the release of nutrients (Ahlgren and Ahlgren 1960; Daubenmire 1968a; Wright and Bailey 1982).

Browse production responded in a manner opposite to the herbaceous components. Twig and leaf production were lower inside the Park than on the controls, despite

displaying higher stem densities. The decrease probably results from the reduced size and vigour of the shrub strata, with the relative amount of twig and leaf growth per live stem being lower. Proportionately larger decreases on both the crest and toe positions on both the burned and unburned areas, suggest that heavier browsing may be occurring at these locations within the landscape. This may relate to their reduced snow cover and closer proximity to the preferred south facing slopes during the winter months. Further decreases were evident on the burned crest where intense burning would have slowed the rate of regrowth (Johnston 1981). Both Bartos and Mueggler (1981) and Brown and Debyle (1989) found that fires with higher intensities resulted in proportionately larger and more prolonged reductions in available browse.

Variability in twig production was substantially less than that in the leaf pool, particularly between topographic positions. This may be attributed to changes in the abundances of shrub species producing the browse. Greater differences in the size, density, and shape of leaves create more variability in leaf production. For example, Symphoricarpos occidentalis leaves are small and thin, and will contribute much less to production than the large, thick, compound leaves of Rubus idaeus.

The lack of significance among differences in total annual production suggests that vegetation pools act in a compensatory manner. A decrease in one vegetative component is likely countered by an increase in one or more of the others as alternate plant species increase in number or size.

6.6 Summary and Management Implications

6.6.1 Summary

This study has effectively utilized multivariate techniques to determine that topographic position, herbivory, and fire were the dominant factors influencing the composition and structure of plant communities in EINP. Furthermore, six distinct community types were documented and could be interpreted with respect to the previous environmental factors.

Position was consistently the most important factor, and was shown to significantly interact with each of the disturbances. In general, north facing slopes were dominated by larger and more mature Populus tremuloides. As a result, herbaceous current annual production was lower, but was partially offset by the higher production of browse from the taller shrub layer. Two community types were documented which were primarily associated with these north facing slopes. They differed from one another only in their location, with one found outside the Park, and the other inside. Although the manipulation of topographic position is unrealistic in resource management, it is important to recognize that other vegetation and ungulate management strategies will depend heavily on position, and in many cases, may be constrained by it.

Herbivory was the second most important environmental factor affecting plant communities, with its impact reflected in their composition, structure, and productivity. Increased herbivory since the Park's establishment appears to be the factor preventing the rejuvenation and spread of Populus tremuloides inside the Park. In addition, grazing has resulted in an increased abundance of non-native invader species such as Poa pratensis, particularly on many of the south facing slopes. This change in species composition likely contributed to the higher current annual production of grass on these sites, and the formation of a unique grassland community type.

Higher browsing pressure inside the Park has reduced shrub heights and current annual browse production inside the Park. The resulting lower shrub stratum is accompanied by a more uniform distribution, and increased current annual production of,

tall herbs such as Calamagrostis canadensis, forming yet another community type. In a somewhat similar community type found outside the Park, a taller, more vigorous shrub stratum underneath a dense, middle aged Populus tremuloides canopy, limits the abundance of many tall herbs. In some locations, shade tolerant, low growing herbs form the major herbaceous component.

Between the disturbances, fire currently appears to be less important from a community perspective, although still affecting the shrub and tree strata, particularly at the crest position. Both tree cover and shrub heights were reduced, while shrub density and the abundance of fire adapted species such as Lathyrus ochroleucus, were higher. Herb current annual production was also highest within the burned area. Fire appeared to be an important factor in the determination of a single community type.

6.6.2 Management Implications

The management of any land area, including that of a national park, depends heavily on the underlying body of knowledge about the natural resources in the area. Information obtained in this study could have several implications for resource managers at EINP. The exact nature of the implications, however, may be limited in reality due to the restrictions imposed by the current policy and objectives of the National Parks Act.

Objectives of the National Parks Act are to preserve and manage both the features and the natural processes representative of the ecosystem found in the moraine of the Beaver Hills (Blyth and Hudson 1987). Tradeoffs will undoubtedly occur whether managing from a vegetative, wildlife, or landscape perspective, because not all individual objectives will be mutually attainable. Ultimately, any management actions will have to consider all of these aspects collectively.

6.6.2.1 Landscape Considerations

Although the data collected in this study was gathered at a local landscape, or ecosite, level, this information can be used to help interpret, with the aid of assumptions, the

ecology of EINP on a broader scale, such as at the ecodistrict and ecoregion level. The main assumption made is that the information collected in this study is generally representative of the Beaver Hills, and therefore, can be compared to other geographical areas. Management of the vegetation in EINP depends in large part on what type of landscape setting is deemed acceptable and desirable to both society and park managers. Several years ago, the Beaver Hills were classed as grassland transition by the Ecoregions Working Group (1989) of Canada. Although Strong (1992) recognized the Beaver Hills as lying in the center of the aspen parkland, he classified the area as an outlier of the low boreal mixedwood ecoregion.

Ecoregions, or ecoclimatic regions, are broad landscape areas characterized by distinctive ecological responses to climate, as expressed by vegetation and reflected in the area's soils, wildlife, and water (Ecoregions Working Group 1989). Climate, in turn, is reflective of characters such as average long term precipitation, temperature, and frost free period, which are determined by factors such as elevation and distance from oceanic waterbodies. Although the Beaver Hills vary in elevation from the surrounding plains, the extent to which this may alter climate remains uncertain, particularly because the concept of a vegetative climax hinges on an accurate understanding of what constitutes 'modal' conditions on that portion of the earth's surface (Daubenmire 1968b). Thus, it could be argued, that if EINP were a prime example of 'transitional grassland', or the parkland ecoregion, the communities found there should differ significantly from that of the boreal mixedwood ecoregion. Furthermore, the climate and growing conditions should differ sufficiently to prevent forest development on at least part of the area. In other words, the prairie influence should be reflected within the Park's natural communities across the landscape, thereby representing topographically driven climaxes, particularly in the absence of disturbance (Daubenmire 1968b). Presumably, changes in microclimate throughout the highly variable topography would be the major cause, such as the presence of hotter, drier conditions on sharp, south facing slopes. The data collected in this study and the work of others (Nicholson 1993), however, tends to support the concept that EINP grades much closer toward the low boreal mixedwood ecoregion. This is further supported by the major difference in dominant soil types found inside the Park (eg.

Luvisols) compared to those found on the surrounding plains (eg. Chernozems). The evidence implies that, climatically, EINP has the same potential to develop into deciduous, and perhaps even coniferous forested vegetation at climax, as do areas north of the Beaver Hills.

Why then, did the vegetation in Elk Island resemble that of an intermittent aspen groveland at the time of park establishment? One of the main reasons was wildfire. Instead of climate, repeated, sporadic disturbance via burning kept the area in a semi-forested, sub-climax 'parkland-like' state, with those areas that were drier burning more often and more intensely resulting in patchy control of the tree cover. The occurrence of Luvisols throughout the Park indicates that burning was probably infrequent enough to allow succession to regularly cover much of the area with forest. With the absence of fire in the twentieth century, forest succession clearly became dominant as was evident outside the Park. This also supports the inclination of Strong (1992) to classify the Beaver Hills as an outlier of the boreal mixedwood. It is also possible that part of the surrounding plains which he classified as parkland, particularly the northern portion, could indeed be subject to forest expansion in the absence of fire, if these lands were not cultivated intensively today.

Another question concerns the actual classification and extent of coverage of the aspen parkland ecoregion. If climate, and not disturbance, is the factor determining the boundaries of an ecoregion, it is possible that the transitional grassland may be more appropriately classified as subunits of the prairie and boreal ecoregions. Only improved climate data at a greater spatial resolution could establish this for certain. These classification subunits, known as ecodistricts, are based in part upon physiographic and geologic patterns (Ecoregions Working Group 1989). The findings of this study support the opinion of Strong (1992), who points out that a much broader and important perspective of ecodistricts is required to deal with macro-topographic features at the provincial level, to which the Beaver Hills belong.

The current landscape inside the Park consists of a mosaic of grassland, shrubland, and forest, which have formed as a result of prescribed fire and decades of intensive ungulate foraging. It appears that many of the grasslands now found in the Park remain

in this state because of the intensity of foraging which inhibits forest encroachment. The effectiveness of prescribed burning in altering the forest cover has also been substantial, but somewhat limited to that part of the landscape where the effects of fire were more pronounced. The complicated relationship of using fire as a tool in landscape and habitat management, indicates that specific, strategic objectives must be set before implementing a burning program.

Managers of EINP are faced with the decision of what type of landscape constitutes a 'natural' feature, as dictated by the Park's objectives. The use of historical evidence to decide this is clearly unreliable, particularly because the time frame for which this information is available is relatively recent, and that arguments for maintaining either a semi-open parkland or a boreal forest are possible. As a result, and given the dynamic history of the vegetation of EINP, it may be more realistic to preserve natural processes rather than natural features.

The two processes that were historically important in altering the landscape were wildfire and variable grazing intensities created by ungulate migrations and wildfire. These are currently most closely represented by the prescribed burning and ungulate trapping programs. Although ungulate harvests are often not perceived as natural per se, this process should be acceptable given that the migrating bison herds which depended on the Beaver Hills during the winter months (Morgan 1980) were harvested by indigenous people. The major difficulty today stems from the lack of animal movement on a regional scale. To achieve true migration and seasonal variation in stocking rates, the Park would have to expand to include a portion of the adjacent plains.

In contrast, prescribed fire is easier to carry out. In the process, a more heterogenous landscape is established, by maintaining a mosaic of forest and grassland cover. The increased variety of community types associated with this condition represents a further increase in biodiversity within the Park. Both community and landscape diversity are important considerations in rangeland conservation management (West 1993).

There is evidence for a natural progression of forested communities towards more open landscapes without the use of fire. This, however, appears to depend on continued high stocking rates which have other, undesirable impacts on the vegetation. Changes in

the abundance and relative composition of shrubs and herbs make this option unrealistic.

A decision not to burn would allow forest succession to take over, provided sufficient recruitment of trees takes place. A reduction in stocking rates would likely be needed to ensure this (Polster and Watson 1979). Forest expansion, however, may produce a forested 'monoculture' over most of the Park's uplands and would result in less diversity on a landscape scale. This in turn would produce less variation among habitat types for wildlife species.

Ultimately, it is important to establish specific target objectives before undergoing any major management changes. The preservation of natural processes and features, should play a major role in deciding future management. It may also be reasonable given the complexity of the landscape ecology in EINP, for managers to give habitat availability, species diversity, and forage productivity, priority over landscape concerns.

6.6.2.2 Vegetation Management Considerations

The composition of plant communities at these sites in EINP were only moderately affected by the disturbances. In particular, most species were found consistently across all disturbances and on at least several topographic positions. One exception which should be noted was in the forest overstories, where mature forms of Amelanchier alnifolia, Prunus pensylvanica, and Prunus virginiana were absent inside the Park. For these species to reach maturity, a reduction in browsing pressure is necessary.

It appears that prescribed burning at present does not remove specific species and, obecause of its variable impact throughout the landscape, may actually increase community diversity. This is because areas such as the north slopes, where burns are less intense, continue to be dominated by the low forb community type while other positions are represented by tall forb communities. Burning therefore appears to be compatible with maintaining diversity among community types and species within the Park.

Although species richness and total diversity were essentially unaffected by the disturbances, invader diversity was much higher inside the Park, particularly on the south aspects. If the objective of Park policy is to maintain maximum species diversity

regardless of the origin of the species, then current management is acceptable. However, if the intent is to minimize the number of invader species within the Park, current management would have to be rated as only partly successful. Past stocking levels of ungulates have been heavy enough to shift many sites in favour of introduced species. Some, such as Poa pratensis, Taraxacum officinale, and Trifolium repens are very competitive and can exclude other, less competitive, native species. In large part, these species can be attributed to human influence. This pattern, evident in EINP, is explained by O'Connor (1991), who suggests that human activity on and around rangelands interrupts migration patterns thereby changing grazing pressure from a seasonal pulse to a regular, systematic cropping. This in turn, favours the establishment of grazing tolerant, invasive species.

The change in vegetation evident on the grassy south facing slopes inside the Park probably represents a fundamental change, wherein the original community crossed an ecological threshold (Figure 25), moving from one successional pathway, or domain, to another (Westoby et al. 1989; Bosch and Kellner 1991). Not only do invader species suppress native vegetation (Wilson 1989), but heavy grazing increases the germination of weedy species (Johnston et al. 1969). Although a reduction in overall stocking rates may decrease the rate at which the remaining native communities are invaded by these species, it is unlikely that those areas already converted would be fully recolonized back to native herbs. Any attempts to re-establish the dominant native grass once found in the area, Festuca scabrella, would be unlikely to succeed given the inability of this species to withstand intensive grazing and competition from established invaders. Further support of this can be found in the permanent monitoring exclosures in the Alberta foothills where Poa pratensis continued to dominate overgrazed rangelands after 40 years of rest from cattle grazing (Willoughby 1993b). Simply decreasing stocking rates is unlikely to offer any solution. Instead, the use of intensive inputs (ie. breaking and reseeding) is probably required to cross back over the threshold (dashed arrow in Figure 25), which was passed when herbivory shifted these sites from one stable domain to another (Friedel 1991; Laycock 1991). These specific practices of range improvement though, are not likely to occur on a widespread scale in an area such as EINP. Nevertheless, burning also

represents a commonly used input (Westoby et al. 1989; George et al. 1992) and can be used to control invader species such as Poa pratensis (Curtis and Partch 1948; Anderson et al. 1970; Hadley 1970). For effective, high intensity fires to be achieved, however, simultaneous reductions in stocking rates would have to be undertaken to accumulate sufficient fuel, particularly on the heavily grazed south facing slopes. The continued use of prescribed fire would also be beneficial by opening up larger areas of grassland and increasing the production of herbaceous forage, thereby alleviating the isolated intensive grazing and limiting the spread of introduced species.

An altogether different management approach would be to redefine invader species as naturalized, thereby recognizing them as an acceptable part of the Park's vegetation and actively incorporating them into the Park's management plans. These species require special management consideration because of their early season of growth, competitive nature, and low forage value in winter. An important part of the Park's overall management plan is an evaluation of range condition (Blyth and Hudson 1987). The traditional method classifies individual species as decreasers, increasers, and invaders, the latter which are absent in the climax vegetation and therefore unacceptable (Stoddart et al. 1975). Unless invader species are included, using this condition classification will find virtually all the south facing slopes investigated in this study to be in poor condition, despite being productive and critical for wildlife use. Only a change in management philosophy including alterations in the overriding policy and mandate of the National Parks Act, would end this trend. These alterations would no doubt create debate because not all invader species would be accepted as naturalized (ie. weedy species), thus requiring decisions as to which species constitute 'weeds'.

Managing for individual species within communities can only be done successfully if their specific responses to disturbances are understood. The variable nature of the EINP landscape and the disturbances found within it, indicates that a more consistent and accurate method of monitoring vegetative change should be adopted. Regular monitoring over prolonged periods within permanently delineated plots distributed throughout the landscape, under both burned and unburned and foraged and unforaged (exclosure) conditions, are required to evaluate the specific response of various plant species to each

disturbance. This information would provide valuable baseline data imperative for making proper management decisions. Several models for establishing benchmark programs already exist including those of the United States Department of Agriculture, the Alberta Forest Service, and Alberta Public Lands.

6.6.2.3 Ungulate Management Considerations

Managing the large herbivores in EINP centers around their dependence of various habitat types. Both prescribed burning and years of intensive foraging have altered the relative amount and distribution of community types as well as their production of browse and herbaceous material.

The early seal vegetation resulting from burning provides better habitat for large ungulates by expanding the food resource and improving the quality of forage (Reynolds 1969). This is particularly true for species which prefer semi-open areas such as wapiti and bison. Forests on the north slopes have a natural resistance to fire which ensures that pockets of cover remain to provide protective and thermal cover. Given that grazing species make up the largest populations in the Park, large scale burning would seem advisable to convert much of the Park to this state, particularly because there is a large increase in forb and grass production associated with this action. Although no net change occurs in the production of browse due to fire, shifts between the dominant types of species may be changing the quality of production. For example, Bisoff (1981) and Renecker and Hudson (1988) found Corylus cornuta to be lower in crude protein compared to many other primary browse species such as Rubus idaeus, Rosa spp., Populus tremuloides, and even Symphoricarpos occidentalis. These depressed levels also appear to be consistent among seasons (Renecker and Hudson 1988), including the important winter period. Bishoff (1981) also concluded that Corylus cornuta is unable to provide ungulates with sufficient phosphorus, even during the summer months. Maintaining a balance among the various forage species available is more likely to meet the dietary requirements of herbivores (Oldemeyer et al. 1977).

In addition to changes in the types of forage species available to wildlife, prescribed

burning can directly improve forage quality. Increases in crude protein and phosphorus have been found in both the shrub and tree regrowth following fire (Debyle et al. 1989).

Burning does have other important implications for wildlife, in addition to those involving forage quality and quantity. For example, an estimated 97% of reproductive female Dermacentor albipictus (winter tick) were killed by prescribed burning in the aspen parkland (Drew et al. 1985). This parasite is a serious pest of moose, making burning a practical option for it's control in a confined area such as EINP.

Widespread burning, however, is not without drawbacks. Reducing the overall area of forest will reduce the amount of leaf fall which is an important source of winter forage for wapiti (Nietfield 1983). Although burned areas are often beneficial for moose, no moose were seen on any of the burned catenas during the lengthy data collection process, suggesting that the area may now be too open for this species. This may be explained by the lack of Populus tremuloides regrowth and high fire frequency because the optimal successional stage for moose is from 11 to 30 years after burning (Bradley et al. 1992). Other ungulate species also require larger forested tracts for cover during critical times such as during severe winter storms and calving. To maintain areas more favourable for these species, some regions would have to be either not burned at all, or burned at lower frequencies, making it critical to have a comprehensive long term burn management plan in place.

Ungulate populations are currently controlled through trapping and removal programs. This is important because foraging has clearly been a major factor in altering the Park's vegetation by limiting stand rejuvenation, altering the growth form of the shrub understory, and reducing browse production.

This latter factor is a key alteration, because while the largest proportion of total production is provided by herbaceous material, most of this is no longer available during the winter months. Early senescence and deterioration in the autumn along with the accumulation of snow can render much of this material inaccessible. Therefore, all ungulates, including bison and wapiti, increase their use and dependence on browse material. Holsworth (1960) found that these two grazing species will increase the amount of browse in their diet up to 30% and 10%, respectively. A further difficulty is that much

of the shrub leaf material is below the snow line. Thus, although twigs make up the smallest part of total production, this component provides the most critical portion of all the forage produced. Twigs are more accessible during the winter and remain higher in nutritive value until late in the dormant season (Stoddart et al. 1975, Bishoff 1981). The result is that an increasing ungulate population may be supported by an excess of herbaceous growth during the summer and fall, while a diminishing browse pool may sustain these same herbivores during the critical winter months. This type of foraging supply and demand pattern is more susceptible to fluctuations which could lead to severe forage shortages. Surges in ungulate populations, heavy snowfalls, poor summer precipitation, or other anomalies, may make this forage production scheme undesirable.

Any manipulation of the shrub layer through burning or other means will have important ramifications on the supply of browse for ungulates. For example, a reduced twig supply would force ungulates to turn to alternate sources of lower quality forage. The implications for management are that larger population reductions may be required to reduce the risk of encountering problems in forage availability. It is currently unknown whether the trend in browse production is increasing or decreasing. This information is clearly necessary in order to monitor forage availability patterns more closely and predict any surpluses and/or shortages.

Another related factor to consider is the role of the south facing slopes inside the Park. The early green up and nutritious herbaceous forage produced may actually be critical in diverting some of the early spring browsing pressure from forested areas. Without the south slopes, even heavier browsing pressures are probable, which would further alter the shrub strata within the Park, particularly because these grasslands are very productive. The main disadvantage of these sites is that the introduced species found here are early curing, and therefore provide poor quality winter forage compared to native species. It would thus seem preferable to limit those areas on which these species dominate because most of the forage use in EINP occurs during the dormant season.

6.7 Additional Research

One of the priorities of national parks, enabling them to resolve the dilemma of how to perpetuate natural forest ecosystems that include fire as a factor of their environment, is to obtain information on fire ecology (Van Wagner 1990). This is required to make affective management decisions. While a large body of information exists for all of North America, little is applicable to EINP because of the area's unique vegetation and climate. The limited amount of information collected on fire ecology in Western Canada to date, particularly with respect to the autecology of specific understory species, leaves much of the baseline data lacking. This information could be collected through the use of long term monitoring programs and tools such as grazing exclosures.

Other gaps which appear in our understanding of the aspen parkland, include establishing a detailed classification of Populus tremuloides forests based on ecological parameters. In addition, information on the rates of conversion of Chernozemic grassland soils to Luvisolic forested soils would be beneficial for determining more accurately the historical ratio between these vegetation types in the EINP landscape. Although this study provides important baseline data, a larger number of stands should be sampled from a wider range of environmental variables to create a more comprehensive and inclusive classification. Additional research could then be directed towards establishing a clearer identity for the parkland, including its position in a broader classification scheme.

Finally, for EINP, a greater understanding must be reached concerning the impact of herbivory and fire throughout the Park. The significant but variable response of plant communities to disturbances within the landscape requires that managers be able to predict how large scale burning or changes in ungulate populations will affect the habitat and forage resources available to ungulates, before they are actually undertaken. In addition, because a goal of herbivore management is to maintain a sustainable system, it is critical to identify the various environmental thresholds within the Park, and manage landscapes so that they are not exceeded (Archer and Smeins 1991). Modelling may prove effective in monitoring the dynamics and responses of both vegetation and ungulates to management strategies in EINP.

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8. APPENDICES

Appendix I: Review of environmental and vegetative data collected.

Environmental Data:	Data Type:	Units:
Level of Herbivory	Nominal (classes)	High & Low
Burn Scorch Height	Continuous (cm/ tree)	Ave. / Transect
Topographic Position	Nominal (classes)	Toe, South, Crest, & North
Slope	Continuous	% / Transect (Ave. of 3)
Soil Type (Great Group)	Nominal (classes)	Orthic Gray Luvisol, Gleyed Gray Luvisol, & Orthic Humic Gleysol
Soil Organic Matter	Continuous	%
Soil pH	Continuous	pH
Soil Texture	Continuous	% Sand, Silt, & Clay
Thickness of Ah	Continuous	cm / Transect
Thickness of Ahe	Continuous	cm / Transect
Thickness of Ae	Continuous	cm / Transect

Vegetative Data :	Method of Data Collection:	Analysis Units:
Tree Density	Stem Counts / Macroplot	# Stems / Hectare
Basal Area (BA)	BA / Tree / Macroplot	Total BA (m^2) / Hectare
Overstory Canopy Cover	Line Intercept Transect (50 m)	% / Transect
Shrub Canopy Cover	Cover / Species / Mesoplots (1 x 1 m)	Ave. % / Transect
Herb Canopy Cover	Cover / Species / Microplots (40 x 50 cm)	Ave. % / Transect

Appendix I (continued): Review of environmental and vegetative data collected.

Vegetative Data :	Method of Data Collection:	Analysis Units:
Diversity Index	From Canopy Covers	Index / Transect
Species Richness	Total # of Species	Species / Transect
Shrub Density	Stem Counts / Microplot	# Stems / m^2
Shrub Height	Maximum Height / Microplot	Ave. Height (cm) / Transect
Current Annual Above Ground Production (Grass, Forb, Twig, & Leaf)	Production / 0.5 m^2 Clip Plot	Ave. Kg / Hectare (Dryweight)

Appendix II: Standard error of the mean's for EINP data.

Stand Factor:	Test Factor:		
	Disturbance	Position	Disturbance x Position
Total Tree Density	149.2	172.3	298.4
Aspen Density	100.4	116.0	200.9
Balsam Density	48.1	55.5	96.1
Total Basal Area	3.10	3.56	6.17
Live Canopy Cover	4.77	5.51	9.54
Total Diversity Index	0.068	0.079	0.137
Invader Diversity Index	0.023	0.026	0.045
Species Richness	1.16	1.34	2.32
Total Shrub Density	0.830	0.959	1.661
Shrub Height Index	2.437	2.814	4.875
Grass Production	43.98	50.78	87.96
Forb Production	53.84	62.16	107.66
Leaf Production	96.24	111.14	192.50
Twig Production	25.94	29.96	51.88
Total Production	128.34	148.18	256.66

Appendix III: Two-way site by species table derived from the analysis of the Elk Island data using TWINSPAN.

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                        Sample Site Number:

                    223333  12122231332   1 11122   1121
Species:            840362486025671545313715379192690824

 6 LONI   INV   21-1-111------------------11-------  000000
18 VIBU   EDU   41-131222122--1------------1--------  000000
52 LINN   BOR   11-------1---------------------------  000000
56 MITE   NUD   11-12311113--------------1-11-------  000000
 5 LONI   DIO   221121131111--11--1----211111-----1-  000001
12 RIBE   TRI   11111311311--1-1-------12-1-1-------  000001
35 CORN   CAN   331333332331--21--3--11-12122-----1-  000001
36 DISP   TRA   3111122222212211121---1--11---------  000001
60 PYRO   ASA   2232412112111-311-11-11111111--1----  000001
 2 CORN   STO   2-----12-1111-12--1-----11----------  000010
20 ACTA   RUB   --1-1-21112--1---2-1--111--1--------  000010
23 ALLI   CER   ---2------------1-------------------  000011
44 GALI   TRI   1111-1-----1-1---1------1---2-------  000011
54 MAIA   CAN   3121211112111-222221111121222-----1-  000011
61 PYRO   CHL   1-1211-----1--1----------1121-------  000011
86 ORYZ   ASP   -1121-----------231----11--1--------  000011
11 RIBE   LAC   11-2-221111---1--------123122--1----  00010
55 MERT   PAN   -11111-1-11--------1---112111--1----  00010
57 PETA   PAL   -3-11211-11-------------12-11--1----  00010
16 SHEP   CAN   -1-2-11212------211-----3-31------1-  00011
48 HERA   LAN   -122-11----1-1-----1-1-1--213--1--1-  00011
63 RUBU   PUB   4443443333332-32-2421224343321121-11  00011
 9 PRUN   PEN   3----------214------1---------------  00100
39 EQUI   ARV   -1-1-----1-3----------1-1-23-------  00100
42 GALE   TET   --1---------11--------------3-------  00100
72 STEL   LON   --1--1-------11----------11-1-------  00100
 4 CRAT   ROT   ---------------33-------------------  001010
67 SMIL   STE   -----------1----1--1----------------  001010
31 CAST   MIN   --------------------------1---------  001011
46 HABE   HYP   -------------------------1----------  001011
58 PETA   SAG   ------------------------1-----------  001011
62 RANU   ACR   ------------------------1-----------  001011
65 SCUT   GAL   ----------------------------2-------  001011
66 SENE   TRI   ------------------------1-----------  001011
76 URTI   DIO   ----------------------------2-------  001011
53 LYSI   CIL   ---1-----------13-312-4------1-----  0011
88 POA   PALU   -----11-------11----2---2---1----1--  0011
92 COV   MOSS   3332323122111111121----112114---13-2  0100
```

Appendix III (continued):

3	CORY	COR	555555555552355555344513251433245 4-	010100
8	POPU	TRE	213333111113121122213121111312111 2-	010100
27	ARAL	NUD	3443444534322544345 3554-44454141-25-	010100
37	EPIL	ANG	------222-211--1---2-13132----12----	010100
50	LATH	OCH	123232342341214122333334222222422 2-	010100
7	POPU	BAL	---11---1--1----------1-11-11--1-1--	010101
13	ROSA	SPP	123434334344454455333444434233443222	010101
14	RUBU	IDA	255534434555555543454453334354443431	010101
17	SYMP	OCC	222222323323344443411224233423444421	010101
28	ASTE	CIL	131322332322221323342424323323243 44-	010101
51	LATH	VEN	-122--3-42-1453433444-22-11133-44-21	010101
64	SANI	MAR	-1221111-112111121131223232311 23--2-	010101
77	VICI	AME	1222222422321-311323344422213334213 1	010101
84	CALA	CAN	123414324351222313455554555335554 43-	010101
1	AMEL	ALN	212431212122342243211232112132223111	01011
10	PRUN	VIR	111321111112243132111 1-2111-12123-11	01011
29	ASTE	CON	2----132224425222-322321--11-32--11-	01011
34	CERA	ARV	----------11---1-11-------------1---	01011
15	SALI	SPP	------1----1---12--1---11-111-11----	011
21	AGAS	FOE	-----------221--23-11112-1-2-2111-1-	011
26	APOC	AND	1---1-11-114432321-2133--121-11-1-11	011
71	STAC	PAL	-----2-----111--11-1211111--11111---	011
79	VIOL	CAN	1-1-1-11-11-1-1-2-11-111--111312-11-	1000
41	FRAG	VIR	-1111211221221112231-112122313221221	10010
43	GALI	BOR	-122123222112223222222331222223332 12	10010
68	SOLI	CAN	--1--2----3323-4132434344534345 5424-	100110
82	BROM	CIL	----1----2-11---1-1------1121--131--	100110
74	THAL	VEN	-122--11--2---1-21-23133111222332-1-	100111
80	AGRO	TRA	-3-1--11---11--1-121--1-1221-21--22-	100111
90	SCHI	PUR	-1-11-1-11------1111-1-21-22-21--12-	100111
22	AGRI	STR	------1----1----1-11---212-33111-22-	10100
33	CIRS	FLO	----------------------------1------1-	10100
47	HALE	DEF	---------------------------1------1--	10100
38	EPIL	CIL	------------------------1------1-----	10101
45	GEUM	ALL	---1------------1------111-1-1-1-1--	10101
70	SONC	ARV	--------------------1--------1------	10101
85	CARE	SPP	--32-11----121--1--221222-1221214214	1011
49	HEIR	UMB	---------1---------1-------1--1--1-1	110
73	TARA	OFF	1--1-11-11-1---131111-1-121212113441	110
89	POA	PRAT	-1-1-----21----3211213242143-5555555	110
91	BARE	SOI	--------------------2-111----2214134	111000
19	ACHI	MIL	----------------1--------111-21-1212	111001
40	ERIG	GLA	----------------------------------2-3	111001
69	SOLI	MIS	-----------------------------------1	111001
78	VIOL	ADU	----------------------------------1-1	111001
87	PHLE	PRA	----------------1-------3-------2123	111001

Appendix III (continued):

```
25 ANTE  PAR  ----------------------------------1--  11101
59 PLAN  MAJ  ------------------------1-----1--211  11101
75 TRIF  REP  -1----------------1--1--1-12--1-2542  11101
81 AGRO  SCA  ----------------------------------1--  11101
24 ANEM  CAN  --------------1-----------1-112-2-1-  1111
30 ASTE  LAE  -------------------------------111----  1111
32 CIRS  ARV  -----------1--------------------11---  1111
83 BROM  INE  ---------------1-------------1-----1  1111

              00000000000000000000000000001111111
              00000000001111111111111111110000001
              00000111111000000011111111111000011
              01111011111000011100000011111
                    00001       00000100001
                                01111
```

Appendix IV: Conceptual soil profile descriptions for Elk Island study.

A. Orthic Gray Luvisol:

Horizon:	Thickness Range:	Comments:
LFH	2 - 9 cm	Scattered charcoal deposits.
Ah	0 - 6 cm	Variable in thickness, granular structure. Color: 10YR 1/1 to 3/2 (moist).
Ahe	2 - 12 cm	Salt & pepper or variable gray appearance. Color: 10YR 2/1 to 4/3 (moist).
Ae	7 - 20 cm	Fine blocky to platy, ashy, friable. Color: 10YR 3/2 to 5/4 (moist) and 10YR 8/1 to 6/3 (dry). May be a few fine mottles: 2.5Y 5/4.
AB	2 - 5 cm	Transitional horizon.
Bt		Prismatic macrostructure, medium to coarse blocky microstructure. Prominent darker colored clay skins. Color: 10YR 3/2 to 4/4 (moist). May be fine mottles: 10YR 4/6 to 5/6.

B. Gleyed Gray Luvisol:

Horizon:	Thickness Range:	Comments:
LFH	5 - 9 cm	Scattered charcoal deposits.
Ah	0 - 4 cm	Variable thickness, irregular border. Color: 10YR 1/1 to 2/2 (moist).
Ahe	3 - 8 cm	Variable border, patchy appearance. Color: 10YR 3/2 to 3/3 (moist).
Ae(g)	10 - 18 cm	Fine platy, silty/ashy when dry. Color: 10YR 3/2 to 5/3 (moist) and 10YR 8/1 to 7/2 (dry). May be mottles: 10YR 4/6 (One soil with a perched water table).
AB	2 - 6 cm	Transitional horizon.
Btgj		Prismatic macrostructure, medium to coarse blocky microstructure. Medium to very thick clay skins. Matrix Color: 10YR 4/2 to 5/3 (moist). Partial gleying evident. Mottle Color: 10YR 4/6 to 5/8 (moist).

Appendix IV (continued):

C. Luvic Gleysol:

Horizon:	Thickness Range:	Comments:
LFH	6 - 14 cm	Scattered charcoal deposits.
Ah	0 - 5 cm	Variable thickness. Color: 10YR 1/1 (moist).
Ahe(g)	6 - 15 cm	Fine blocky to platy, few mottles. Color: 10YR 2/1 to 3/4 (moist); 10YR 4/2 (dry). Mottle Color: 10YR 5/8 to 6/8 (moist).
Ae(g)	8 - 20 cm	Fine to coarse platy, ashy appearance. Color: 10YR 2/1 to 5/3 (moist) and 10YR 7/1 to 4/2 (dry). Mottle Color: 10YR 5/6 to 5/8.
AB(g)	2 - 6 cm	Transitional horizon.
Btg		Prominent gleying conditions and mottling, medium to coarse blocky structure, thick clay skins evident. Matrix Color: 10YR 3/2 to 5/2 (moist). Mottle Color: 10YR 4/6 to 5/8 (moist).

Appendix V: Soil horizon thicknesses, soil pH, and organic matter by disturbance and position.

	Horizon Thickness (cm):				Organic Matter:
	Ah	Ahe	Ae	pH	(%)
Disturbance:	P=0.189	P=0.159	P=0.259	P=0.406	P=0.021
Burned	2.33 a	5.58 a	13.83 a	5.86 a	5.56 a
Unburned	0.92 a	4.83 a	11.75 a	6.14 a	3.67 b
Control	2.08 a	7.25 a	13.33 a	6.22 a	6.41 a
Position:	P=0.167	P=0.070	P=0.188	P=0.015	P=0.035
Toe	2.89 a	7.56 a	14.78 a	6.36 a	5.77 a
South	1.78 a b	7.22 a	11.22 a	6.30 a b	5.99 a
Crest	1.33 a b	4.78 a b	11.89 a	5.73 c	5.02 a b
North	1.11 b	4.00 b	14.0 a	5.89 b c	4.08 b
Dist. x Position:	P=0.689	P=0.388	P=0.963	P=0.866	P=0.324
Toe x Burned	3.0 a	5.3 b	16.0 a	6.04 a	5.53 b
Toe x Unburned	3.0 a	6.0 a b	14.3 a	6.31 a	3.58 b
Toe x Control	2.7 a	11.3 a	14.0 a	6.73 a	8.21 a
South x Burned	2.7 a	7.0 a	11.3 a	6.15 a	7.02 a
South x Unburned	0 a	5.0 a	10.3 a	6.35 a	4.91 a
South x Control	2.7 a	9.7 a	12.0 a	6.39 a	6.03 a
Crest x Burned	1.3 a	5.0 a	13.3 a	5.48 a	5.61 a
Crest x Unburned	0.7 a	4.3 a	10.7 a	5.80 a	3.25 b
Crest x Control	2.0 a	5.0 a	11.7 a	5.90 a	6.20 a
North x Burned	2.3 a	5.0 a	14.7 a	5.75 a	4.08 a
North x Unburned	0 a	4.0 a	11.7 a	6.09 a	2.94 a
North x Control	1.0 a	3.0 a	15.7 a	5.83 a	5.22 a

Means represented by the same letter are not significantly different at P=0.05 using the Least Significant Difference test.
Interaction comparisons are between disturbances and within positions.